Hydrological variation along the Missouri River and its effect on the fish community

by

Mark Alan Pegg

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Preface

Population Structure and Habitat Use of Benthic Fishes along the Missouri and Lower Yellowstone Rivers

This research is reported in 12 volumes. Final Report volumes are listed below and are available from the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15" Street, Omaha, NE 68102 (rebecca.j.latka@usace.army.mil, 4021221-4602) for copies. Volumes are currently available unless indicated otherwise (anticipated date of publication).

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Final Report: Project Volumes

Berry, C. R. and B. A. Young. 2001. Introduction to the benthic fishes study. Volume 1 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers. U. S. Geological Survey, Cooperative Research Units, South Dakota State University, Box 2140b, Brookings, South Dakota 57007. charles_berry@sdstate.edu

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Welker, T. L. 2000. Ecology and structure of fish communities in the Missouri and lower Yellowstone rivers. University of Idaho. Volume 12 of Population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone rivers.

Outreach Product

Berry, C. and D. Galat. 2001. Synopsis of the population structure and habitat use of benthic fishes along the Missouri and Lower Yellowstone rivers. Agriculture Experiment Station Bulletin 7xx, Available from: Bulletin Room, LMHl12, South Dakota State University, Brookings, South Dakota 57007. (available August 2001)

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CHAPTER 1. GENERAL INTRODUCTION

Introduction

The Missouri River is the longest river in the United States stretching nearly 4,400 km from western Montana to its confluence with the Mississippi river in Missouri. The Missouri River system is also one of the largest drainages in North America as it drains nearly one-sixth of the total area of the United States (Berner 1951). The Missouri River was characterized as a meandering, turbid river laden with islands prior to alteration in the mid-1900s (Funk and Robinson 1974). Flow management, however, has changed much of the lower two-thirds of the river. Reservoirs built in the middle portion of the Missouri River have created a more lacustrine habitat; whereas, in the lower reaches, channelization efforts have made the river a relatively narrow, swift channel.

Human use of the Missouri River has a long history that can be traced to well beyond that of the Lewis and Clark expedition in the early 1800s. However, the more modern methods used to control the river in the early to mid-1900s has had the largest affect. Channelization of the river from the confluence with the Mississippi River to Sioux City, IA, was authorized to allow passage of deep-barge traffic as an alternative to railroads (Schneiders 1996). The actual channelization project lasted over 40 years (1927 - 1969) and has changed a river that was once diverse in habitat, meandering, and well connected with its floodplain to one that is relatively uniform. The channelized portion of the river was actually shortened by 125 km and lost nearly 64% of the wetted area (Whitley and Campbell 1974).

Additional concern also arose about controlling spring floods and storing water within the basin for times of need so six mainstem impoundments were constructed between 1937 and 1963 (USACOE 1994). Over one-half of the upper 2,500 km of the Missouri River was impounded upon completion of the final dam (Morris et al. 1968). The river was then effectively divided into three hydrological zones. The upstream most zone, being least altered, has historically had the least amount of human influence. The middle, inter-reservoir zones and the lower channelized zone however, have been heavily impacted by human needs.

Flow modifications are commonplace human disruptions to river and stream environments (Bain et al. 1988). These disruptions can have serious effects on the fish and wildlife species who are dependent upon unaltered conditions to survive. The Missouri River is no exception in this regard as many native fish populations are thought to be in general decline throughout the river (Hesse 1996). One native Missouri River fish species, pallid sturgeon Scaphirhynchus albus, is already federally endangered and there could be as many as 20 others along the river that may be threatened (Whitmore and Keenlyne 1990). This includes species such as paddlefish Polydon spatula, blue sucker Cycleptus elongatus, sturgeon chub Macrhybopsis gelida, sicklefin chub M. meeki, flathead chub Platygobio gracilis, and two species of the genus Hybognathus. Many of these at risk species are strongly associated with the benthic habitat throughout the system thus indicating more information on this subset of native species was warranted. With the exception of a few sport and commercial fish species, the benthic fish community along the Missouri River has rarely been studied (Russell 1965; Kallemeyn and Novotny 1977; Latka et al. 1995). This lack of information prompted the U.S. Army Corps of Engineers to initiate a river-wide study of the benthic fish community.

The scope of this project was to collect broad baseline data, over a three year period (1996 - 1998), to assess the population and community attributes (e.g., habitat use, recruitment, relative abundance, age structure, growth, and condition) of fish specifically identified as a member of the benthic fish guild. Here, the benthic fish guild was defined as those species having life history characteristics that generally require an association with the benthic zone for a large portion of their lives. A consortium of U.S. Geological Survey (USGS), Biological Resources Division (BRD), Cooperative Fish and Wildlife Research Units (Iowa, Kansas, Missouri, Montana, South Dakota), Montana Fish, Wildlife and Parks, the University of Idaho, and the USGS-BRD Columbia Environmental Research Center, here after referred to as the Missouri River Benthic Fish Project (MRBFP), designed and implemented this project. Each agency/university sampled a unique section of river and collected both physical and biological information on the benthic fish community following standardized methods (Sappington et al. 1998). Our primary sampling efforts were focused only on the riverine reaches of the Missouri and lower Yellowstone Rivers and these data were then used to assist the Corps of Engineers in development of water management plans that would be beneficial to the benthic fishes along the Missouri River.

Beyond the confines of this project, graduate students at each university were required to develop more specific research topics. My research was directed towards three broad areas. First, I was interested in how flows have changed through various management practices and assessment of the current flow conditions. Secondly, I was also interested in how well the current flow regime can be used to describe fish community structure throughout the river system. Finally, because the consortium collected age and growth information, I also wanted to capitalize on these data to investigate the potential for latitudinal effects in fish growth rates. My specific objectives were to 1) evaluate the influences of past human management practices on the hydrograph of the Missouri River by comparing pre- and post-alteration flow conditions; 2) identify and group reaches that are subjected to similar, post-alteration flow conditions, 3) determine if there was a relation between these flow units and fish community structure found throughout the river; and 4) determine if there are latitudinal or other large scale patterns in the growth rates from fish caught in different sections of the river.

Dissertation Organization

This dissertation is comprised of a General Introduction, four manuscripts prepared for submission to Regulated Rivers: Research and Management (Chapters 2-3), Ecological Applications (Chapter 4), and Transactions of the American Fisheries Society (Chapter 5), and a General Conclusion (Chapter 6). All sections were written by M.A. Pegg and edited by C.L. Pierce.

The first manuscript "Effects of Channelization and Impoundment on Flow in the Missouri River: a Time Series Analysis of Daily Mean Flow" compares daily mean flows between the pre-alteration period (1923-1948) and post-alteration period (1966-1996) for ten Missouri River gauge stations. Included in this chapter is a quantitative assessment of how these flows differ between the two periods.

The second manuscript "Classification of Reaches in the Missouri and Lower Yellowstone Rivers Based on Flow Characteristics" focuses on identifying unique flow units using a suite of hydrological variables and focuses specifically on present flow conditions.

The third manuscript "Fish Community Structure Comparisons Within and Among Distinct Hydrological Units from the Missouri and lower Yellowstone Rivers" builds upon the flow units identified in the previous chapter and explores how the fish community structures vary based on these flow characteristics.

The final manuscript "Growth Rate Responses of Missouri and Lower Yellowstone River Fishes to a Latitudinal Gradient" compares growth rates among several reaches for five Missouri River species. Large-scale spatial trends in these growth rates are discussed.

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CHAPTER 2. EFFECTS OF CHANNELIZATION AND IMPOUNDMENT ON FLOW IN THE MISSOURI RIVER: A TIME SERIES ANALYSIS OF DAILY MEAN FLOW

A paper to be submitted to Regulated Rivers: Research and Management

Mark A. Pegg, Clay L. Pierce, and Anindya Roy

Abstract. Human alteration of large rivers is commonplace, often resulting in significant changes in flow characteristics. We used a time series approach to examine daily mean flow data from locations throughout the mainstem Missouri River and tested for differences associated with human alteration. Data from a pre-alteration period (1925-1948) were compared with a post-alteration period (1967-1996), and separate analyses were conducted using either data from the entire year or restricted to the spring fish spawning period (1 April - 30 June). Daily mean flow over the entire year was significantly higher during the post-alteration period at all locations, largely reflecting long-term differences in precipitation. Flow during the spring was significantly lower during the post-alteration period at the most highly altered locations in the middle portion of the river, but unchanged at the least altered locations in the upper and lower portions. A natural flow regime during spring is widely viewed as beneficial to fish populations and river-floodplain ecosystems. Our results suggest that human alterations on the Missouri River, particularly in the middle

portion most strongly affected by impoundments and channelization, have resulted in changes to the natural spring flow regime.

Introduction

Human activities have altered the flow of large rivers for thousands of years (Petts et al. 1989). Lotic systems have been modified worldwide to provide flood control, navigation, water supply, power generation, and recreation needs. While there have been benefits to these management practices, there have also been costs. Modification to both river and riparian habitats can range from the relatively localized effects of small-scale grazing to the much broader effects of channelization and impoundment. As a result, many of the original defining physical and ecological characteristics of these managed systems have been profoundly altered (Poff et al. 1997).

Altered flow has been one of the primary consequences of impoundment and channelization. Impoundments designed primarily for flood control, navigation, and water supply tend to dampen natural flow variation by storing large amounts of water for later, controlled release (Bravard and Petts 1996). Conversely, dams built for power generation tend to accentuate natural variability by creating daily high and low flow periods to meet electrical demands (Bravard and Petts 1996). Another potential consequence of impoundment is a change in the response of daily flows to rainfall, snowmelt, groundwater, and other natural delivery processes. Changing these processes can influence the timing and magnitude of flows throughout the year, which in turn can have serious affects on the biological community that has evolved in, and may be dependent upon, natural flow conditions (Poff et al. 1997).

Channelization, accomplished by armoring the shorelines, diverting water out of side channels, and straightening the channel itself, also influences flow by facilitating rapid transport of water downstream. Other direct consequences of channelization include loss of river connectivity to the floodplain (Ward and Stanford 1995), changes in water quality (Whitley and Campbell 1974), and loss of aquatic habitat (Mosley 1983).

Flow in many large river systems is affected by a combination of alterations, including impoundments, channelized reaches, water diversions, and numerous landscape changes in the catchment. These alterations are likely to result in complex changes to the flow regime, and the precise nature of these changes may be difficult to predict. Flow reductions in impounded reaches, increased velocities in channelized reaches, loss of diverse habitat complexes, changes in runoff and sedimentation loading rates, and altered nutrient cycles, all a result of human alteration, create an environment seldom if ever experienced in these lotic systems (Ligon et al. 1995; Ibanez et al. 1996).

Stream flow is one of the driving variables that defines the distribution and abundance of biological communities in lotic systems (Poff et al. 1997). Biological responses to flow management include changes in aquatic (Schmulbach et al. 1975; Travnichek and Meceina 1994; Parasiewicz et al. 1998; Ponton and Vauchel 1998; Ruiz 1998) and terrestrial (Reily and Johnson 1982; Nilsson et al. 1991; Toner and Keddy 1997) community structure, and invasion and establishment of exotic species (Patton and Hubert 1993), all of which have been documented throughout the world (Mosely 1983; Bain et al. 1988; Maheshwari 1995;

Ibanez et al. 1996; Poff et al. 1997; Steiger et al. 1998). In large rivers, one of the most well documented influences of flow has been the role of spring flooding in providing suitable spawning conditions and nursery habitat for fishes (Junk et al. 1989).

Poff et al. (1997) identified magnitude of discharge, frequency of flow extremes, duration of a given flow condition, timing of extremes, and the rate of change from one flow to another (flashiness) as major flow components that regulate ecological processes. All or part of these five components have been used to evaluate various aspects of how flow has changed before and after large-scale management in lotic systems (Richter et al. 1996; Richter et al. 1997; Galat and Lipkin 2000). Most of these studies ultimately used monthly or annual summary statistics of flow conditions at several gauge stations to characterize the degree of hydrological alteration. In contrast, quantitative descriptions of patterns of daily flows using long-term data have not been attempted. Testing for differences in flow patterns resulting from human alterations requires data from before as well as after the alterations, a requirement that is often unfulfilled. Fortunately, long historical records of flow exist for some large rivers, permitting detailed analysis of patterns of daily flow before and after human alteration.

Time series analyses are ideally suited for flow data because they are generally reported at equally spaced, discrete time intervals (e.g., annual, monthly, daily). Common applications of hydrologic time series analyses include studying long-term trends, wet/dry cycles, predicting future water use, and identifying changes to flows induced by environmental shifts or human activity (Yevjevich 1984). Time series models can also provide the basis for probability estimation and testing for significant differences in flow between different periods of time, such as before and after human alteration.

The Missouri River is one of the largest rivers in North America, stretching over 4,000 km and draining about one sixth of the continental United States (Figure 1). Historically, the Missouri River was characterized as a very turbid, meandering river as it flowed through the Great Plains of North America (Berner 1951; Funk and Robinson 1974). However, the onset of large-scale alteration in the early to mid-1900s on the Missouri River has dramatically altered the pre-European settlement condition of this large floodplain river (Hesse 1987). Channelization of the lower river, implemented to allow deep-draft barge traffic as a means of competition with railroads from the river's confluence with the Mississippi River to Sioux City, Iowa, was accomplished between 1927 and 1969 (Schneiders 1996). A series of six mainstem dams were also constructed between 1937 and 1963, primarily to control flooding and to provide adequate water depths for navigation on the lower river (Galat et al. 1996). The associated reservoirs cover nearly half of the upper 2,500 km of the Missouri River (Morris et al. 1968). The result of these alterations has been a metamorphosis from a once complex floodplain river into a relatively artificial system (Whitley and Campbell 1974), and division of the river into three zones: an upper, relatively unaltered area above the reservoirs, areas between the reservoirs where short stretches of unchannelized river remain, and a lower, channelized area (Figure 1).

The purpose of this study was to collect and examine daily mean flow data from locations throughout the mainstem Missouri River, and to test for differences that could be associated with human alteration. Our specific objectives were to: 1) develop time series models of daily mean flow for ten Missouri River locations with data series encompassing pre- and post-alteration periods, 2) test for significant differences in daily mean flow between pre- and post-alteration periods using data from the entire year, and 3) test for differences in daily mean flow between pre- and post-alteration periods using data restricted to the spring fish spawning season.

Methods

Flow Data

We obtained daily mean flow data for Missouri River gauge stations from the U.S. Geological Survey (USGS) on-line data base, and divided the data set into pre-alteration and post-alteration periods for further analysis. Construction of the impoundments and channelization primarily occurred between water year (October - September) 1948 through water year 1966 as the five lower reservoirs were being constructed and in the process of filling (Galat et al. 1996). We did not include these years in our analysis due to the potential influence of this 'filling effect' on flow. Thus, we considered data from before 1948 as pre-alteration and that after 1966 as post-alteration data.

The data record available during the pre-alteration period varied among stations, with some stations having only a few years (10-15), whereas one station had nearly 60 years of record. Comparing time series of different lengths is possible, but simultaneous evaluation of several gauge stations along the length of the river is facilitated by making all data series similar lengths. The outcome is a slight loss of information, but the advantage is that the resulting series generally reflect the same chronological sequence of large-scale natural phenomena (e.g., drought, flood). Therefore, we only used gauge stations that provided information for at least 18 of the 23 years immediately prior to 1948 and data prior to 1925 were dropped from our analyses. These procedures yielded acceptable data sets from ten gauge stations distributed throughout the mainstem Missouri River, and representing the three zones with varying degrees of human alteration (Figure 1).

Statistical Analyses

Daily mean flows for each gauge station were individually assessed for differences between the pre- and post-alteration period at the annual and spring fish spawning season scales. We first fit individual time series models for every gauge station following established methods to identify the appropriate time series model for each period and gauge station combination (Appendix 1; Box and Jenkins 1970; Wei 1990). We then combined the two models, using weighted least-squares regression, to directly test for differences in daily mean flows between the two periods. Next, we used the results from these ten gauge stations to evaluate patterns in flow throughout the river.

Results

Daily Flows Over the Entire Year

Figure 2 illustrates the daily mean flows for pre- and post-alteration periods at four gauge stations representative of the major Missouri River flow patterns observed in our analyses. Visual inspection suggests that flows in the middle reaches of the river have changed dramatically between the pre- and post-alteration periods; in particular the range of variability was drastically reduced during the post-alteration period. In contrast, the ranges of variability appear similar between the two periods at Fort Benton, the uppermost station, and Hermann, the lowermost station on the Missouri River (Figure 1,2).

An autoregressive model with two lagged coefficients (AR(2) model) fit to the transformed data adequately defined the flow patterns for all gauge stations and in both time periods. Autocorrelation and periodicity were generally removed by the transformation as indicated by the residual values in our models (Figure 3). As with the mean values (Figure 2), the amount of variability in the residual plots is lower after alteration through the inter-reservoir and upper channelized reaches of the river as represented by Bismarck, ND and Omaha, NE (Figure 3). Conversely, in the extreme upper and lower portions of the river, the residual variability appears to be similar in pre- and post-alteration periods. However, daily mean flows were significantly higher during the post-alteration period at all gauge stations ($P < 0.01$; Table 1). Post-alteration daily flows averaged 16 percent higher than the pre-alteration flows at Bismarck, ND and 10 percent higher at Yankton, SD. The remaining stations had daily mean flows during the post-alteration period that averaged from 30 to 45 percent higher than pre-alteration flows.

Daily Flows During the Spring Fish Spawning Period

The graphical comparisons of pre- and post-alteration daily mean flows during the spring fish spawning season were qualitatively similar to those made over the entire year, with the most obvious changes appearing in the middle sections of the river (Figure 4). AR(2) models provided adequate fits, and residual plots were similar to those in Figure 3.

Average percent differences between the two periods ranged from two to 32 percent which were generally lower than average differences over the entire year. Tests for differences between pre- and post-alteration yielded quite different results compared to the annual scale (Table 2). Post-alteration, spring daily mean flows at the two uppermost stations (Fort Benton, MT and Wolf Point, MT) and the two lower most stations (Boonville, MO and Herman, MO) were not significantly different between the two time periods (Table 2). In contrast, stations located in the middle portion of the river (Bismarck, ND to Kansas City, MO) did significantly differ ($P < 0.10$), but showed no consistent trend above or below pre-alteration estimates during the post-alteration period. Spring spawning daily flows at Bismarck, ND averaged 32 percent lower, Yankton, SD averaged 28 percent lower, and Omaha, NE averaged 5 percent lower during the post-alteration period; whereas, flows from Nebraska City, NE to Kansas City, MO averaged 5 to 7 percent higher during the post-alteration period.

Discussion

Our tests have shown that the Missouri River daily flows have changed over time. These changes indicate that the nature of the daily mean flows have changed beyond the natural variation generally associated with annual or seasonal flow cycles between the two time periods. Consequently, daily mean flows were significantly higher during the post-alteration period at all gauge stations when analyzed at the annual scale. There were also significant differences at the most strongly human influenced gauge stations during the spring flow period (Table 2). These findings concur with those of Galat and Lipkin (2000) who reported higher mean annual discharges along the Missouri River for the post-alteration period using a different statistical approach. Many factors could have influenced the changes between these two periods ranging from climatological shifts to water management practices.

A shift in the amount of annual precipitation entering the Missouri River basin could easily change daily mean flows between these two periods. Indeed, the United States had severe droughts during the 1930s and 1940s. Conversely, the 1990s have been some of the wetter years on record for the Missouri River Basin. Hu et al. (1998) reported that the amount of annual precipitation generally declined through about the mid 1960s and then began an upward trend in the lower Missouri River basin states of Nebraska, Kansas, and Missouri. This change in annual precipitation, coupled with the managed water releases from the impoundments, seems a likely basis for the different daily mean flow values between the two periods in the lower portion of the river (Figure 2).

The trend for higher precipitation rates does not persist throughout the entire basin however. Karl et al. (1996) reported that while the national trend over the past century has been for a slight increase in precipitation, the upper Missouri River states of Montana, Wyoming, and North Dakota have experienced a decline. This result conflicts with our finding of higher daily mean flows on an annual basis throughout the river system. Therefore, we must further investigate other possible explanations on how and why flows are higher in the post-alteration period.

Flow regulation may also have played a role in creating different hydrographs between the two periods. The mainstem reservoirs were created, in part, for flood control and support of navigation (USACOE 1994). This requires water to be held back in the spring, when normal flooding historically occurred, for use in sustained releases later in the summer and fall when water is not sufficiently available. Long-term retention of runoff in these reservoirs may also contribute to higher mean flows during above average precipitation years because water is released at a higher than normal rate in an attempt to return the reservoirs to their prescribed levels. However, because water is held back in the spring, we would expect the spring spawning flows in the inter-reservoir reaches to be lower than the pre-alteration period as a consequence of this holding effect. Our findings support this prediction in that the Bismarck, ND and Yankton, SD gauge stations (Figure 1) experienced a marked decrease in spring fish spawning flows during the post-alteration period. The Omaha, NE station also experienced slightly lower spring fish spawning flows, indicating that the river is still influenced by the reservoir operations roughly 250 km downstream of the last impoundment. Moving downstream from these impoundments appears to mediate flow differences between the two periods due to input from relatively large tributaries (Chapter 3; Galat and Lipkin 2000).

The spring flow period is important to the ecology of large rivers and is an area of strong concern when addressing biological problems throughout the Missouri River system (Galat et al. 1996). The flood-pulse concept (FPC; Junk et al. 1989) is based on the theory that biological communities in large floodplain rivers have evolved to depend on the timing, duration, and water level changes generally associated with spring flooding. These spates trigger fish spawning events and provide food and nursery areas in addition to maintaining diversity within the system (Johnson et al. 1995). When these flooding bouts are removed from the system, as seen here in the middle reaches of the river, basic biological functions such as spawning and recruitment can be curtailed causing negative responses in diversity and density of the native species. Therefore, it may be important to attempt to return the spring flow regime to one resembling that of the pre-alteration period. Our finding that the uppermost and lowermost reaches showed no significant change between the two alteration periods provides evidence that the natural spring flow regime, that existed throughout the river prior to alteration, is still prevalent in these two reaches. We can then use this information as a reference to restore a more natural spring hydrograph to the middle reach of the river.

Impoundment and channelization has also disconnected about the lower two thirds of the Missouri River from its floodplain. According to the FPC, loss of connectivity can have detrimental affects. Floodplain rivers are dynamic systems that rely heavily on the interactions between both the river and the floodplain to properly function (Ward and Stanford 1995). Many aquatic and terrestrial organisms use the inundated areas of the floodplain during overbank flows. In fact, fish production from the floodplain can be a major source of biomass (Ward and Stanford 1995) and recruitment (Jackson 1993) to the main channel areas once flood waters have receded. Spring fish spawning flows along the middle one-third of the Missouri River were lower in the post-alteration period limiting the number of overbank flows needed to maintain connectivity. Blocking this natural process thus restricts the available habitat to main channel areas and there is some evidence that the fish communities have changed after closure of the impoundments (Morris et al. 1968; Funk and Robinson 1974; Whitley and Campbell 1974; Schmulbach et al. 1975). Whitley and Campbell (1974) summarized several studies showing a decline in fish species diversity that could be a result of impoundment and channelization. Reily and Johnson (1982) suggested that terrestrial organisms have also been impacted by the change in natural flows where they reported a change in species composition of floodplain forests along the Missouri River due to a lowering water table and the lack of annual floodplain inundations. Our results, showing that the middle portion of the Missouri River is most affected by human alteration, suggest that overbank flooding during the crucial spring spawning period may assist in conserving or restoring native aquatic and terrestrial communities.

The management practices imposed on the Missouri River may also have an affect on the longitudinal diversity of aquatic communities. Pristine streams and rivers should exhibit a continual gradient in physical, and ultimately biological, parameters from upstream to downstream areas (Vannote et al. 1980). However, this natural longitudinal succession is clouded by human induced impacts (Statzner and Higler 1986). Water released from impoundments has been dramatically changed by the settling of both sediment and nutrients in the reservoir. Therefore, placement of impoundments in traditionally nutrient and sediment rich river reaches can shift the water quality parameters of the outflowing water to that of headwater areas upstream. Fish and other aquatic organisms immediately below these impoundments cannot cope with the new environmental conditions and are eventually displaced causing a discontinuity in the latitudinal gradient of diversity along the river system. There is some evidence that this discontinuity has had an influence on the fish communities along the Missouri River. Species richness and community structure of riverine fish communities in the upper and middle two-thirds of the river were similar compared to the lower one-third of the river suggesting that the impoundments have influenced the river continuum (Chapter 4).

Analyses from studies investigating other aspects of flow on the Missouri River have generally reached similar conclusions that the middle portion of the river has been most altered. Using a suite of summary statistics over a similar time period, Galat and Lipkin (2000) found that the relatively unaltered areas of the upper Missouri River, and to some extent the lower 600 km before joining the Mississippi River, maintained a certain degree of natural variability after impoundment; whereas, the middle portion of the river was substantially altered. Similarly, Pegg and Pierce (Chapter 3) reported that the upper and lower extreme river reaches of the Missouri River were more statistically similar to each other than to some of the reaches that were geographically closer, but heavily influenced by water management practices. Coupling these findings with our study suggests a consistent trend in flow alteration that is most pronounced in the middle portion of the river. This trend could have a profound influence on how we view the river. Knowing that the middle portion of the river has felt the largest impact of channelization and impoundment, research and flow mitigation efforts could be appropriately directed at this area to protect and conserve the biological communities.

There is little doubt that the Missouri River flow regime has changed between the pre-alteration and post-alteration periods. Identifying the specific cause of these changes is clouded by the interaction of both natural phenomena and human alterations. Hydrology is not solely responsible for the structure of the biological community within this system but does play an important role and changes can therefore have serious physical and biological implications. It is not likely that the river will be returned to its pre-alteration state. This is partly due to the fact that not all of the changes are necessarily anthropogenic and partly because the multipurpose uses of the river for flood control, hydropower generation, navigation, irrigation, conservation of fish and wildlife species, and recreation occasionally conflict and are given different priorities. However, providing a hydrograph similar to the pre-alteration period at sites most greatly affected during spring flows may be a starting point to mediate some of the declining trends in aquatic and terrestrial communities that are now being reported along the Missouri River.

APPENDIX 1. TIME SERIES METHODS

Simply stated, a time series is a procession of observations. Each time series is characterized by a deterministic element, a stochastic element, or a combination of the two (Wei 1990). The deterministic element can consist of periodic, seasonal, cyclic, increasing/decreasing trend, sudden change (jump), or any combination of these components (Haan 1977). These deterministic components create nonconstant means and/or variances resulting in a situation referred to as nonstationarity. Time series applications deal predominantly with stationary series, so nonstationarity is undesirable (i.e., constant mean and variance; SAS 1991). Fortunately, nonstationarity can be accounted for through transformation and differencing techniques.

Our intent here is to provide only a brief summary of our time series methods rather than a comprehensive overview. For further details, see Yevjevich (1984), Wei (1990), or SAS (1991). We followed the Box-Jenkins (Box and Jenkins 1970) approach to identify the best time series model. This requires identification of the underlying process, estimation of model parameters, and diagnostic checks for goodness of fit. The identification procedure attempted to identify the process by which the series is driven. Estimates of the model parameters were then tentatively determined after the underlying process was identified. Diagnostic checks, in the form of autocorrelation plots, residual plots, and evaluating summary statistics (e.g., Akaike's Information Criterion, Durbin-Watson statistic), were used to assess the model parameters. These steps were repeated until the best fitting model was identified.

We first fit individual time series models to each alteration period for every gauge station. Autoregressive (AR) models estimate a process, where the present observation relies upon prior observations to estimate its current value (Wei 1990). Daily mean flows tend to be dependent upon prior flows making AR models appropriate (Yevjevich 1984). The general structure of an AR model is:

$$y_t = \theta_0 + \phi_1 y_{t-1} + \ldots + \phi_p y_{t-p} + a_t,$$

where y_t is the observed value at time t; θ_0 is a constant; values of ϕ are the model coefficients which relate the proportional effect that each previous (lagged) observation has on y_t; p is the total number of lags; and a_t is a random error term.

Multiple year hydrological data tend to be nonstationary due to periodicities corresponding to seasonal fluctuations. We accounted for nonstationarity by using several sine/cosine transformations of the time variable to describe the flow characteristics at each station, where each data point had a series of paired transformations calculated as:

$$\sin(x) = \sin(x*2\pi*t/d) \qquad \text{and} \qquad \cos(x) = \cos(x*2\pi*t/d)$$

where x is the sequence number of the transformation (i.e., 1 for the first sin/cos transformation, 2 for the second, etc.), t is the time variable, and d is the number of days in one full period of record (here d = 365). We also used a variable time coefficient in the modeling process because the variances remained somewhat unequal through time after transformation.

We used the AUTOREG (SAS 1991) procedure to fit an initial AR and assessed the autocorrelation function (acf) to identify the number of parameters needed in each model. After model identification, we examined the residuals to verify that there was no remaining correlation. We then individually tested each gauge station against the hypothesis that daily mean flows were different between the two periods. We created an individual matrix for each flow period from the resulting time series models that included the sine/cosine transformed data and appropriate number of lagged flow values from the model. We then multiplied the pre- and post-alteration matrices using a weighted least-squares regression approach, with the reciprocal of the variance (SAS 1988) from the original AR model as our weighting factor. This regression allowed us to make paired comparisons between the pre- and post-alteration period at each gauge station because we could estimate the mean and standard deviation through the matrix multiplication process.

We also tested for differences in daily mean flows between the pre- and post-alteration periods for the spring fish spawning period between 1 April and 30 June. Our analyses were similar, with the exception that the variable d used in the sine/cosine transformations was changed to reflect the number of days in the spring flow period (d= 91).

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Table 1. Summary of tests for differences in daily mean flows between pre- and post-alteration periods on the Missouri River, using data from the entire year. Gauge stations were tested individually.

Gauge Station		Variance	Degrees of Freedom	F	P
Fort Benton, MT	Pre:	662641	12 19,691	4.66	0.0001
	Post:	522393			
Wolf Point, MT	Pre:	424168	12 18,595	3.79	0.0001
	Post:	291058			
Bismarck, ND	Pre:	21432690	12 18,413	10.08	0.0001
	Post:	1487294			
Yankton, SD	Pre:	23953464	12 16,392	6.52	0.0001
	Post:	1194356			
Omaha, NE	Pre:	18721078	12 18,625	10.74	0.0001
	Post:	5044982			
Nebraska City, NE	Pre:	23154802	12 18,281	9.30	0.0001
	Post:	10794799			
St. Joseph, MO	Pre:	35413740	12 18,230	8.57	0.0001
	Post:	38091531			
Kansas City, MO	Pre:	48446994	12 18,230	5.31	0.0001
	Post:	54745238			
Boonville, MO	Pre:	58861355	12 19,326	3.45	0.0001
	Post:	84368759			
Herman, MO	Pre:	100550000	12 18,229	1.91	0.028
	Post:	130350000			

Table 2. Summary of tests for differences in daily mean flow between pre- and post-alteration periods on the Missouri River, using data restricted to the spring spawning season. Gauge stations were tested individually.

Gauge Station		Variance	Degrees of Freedom	*F*	*P*
Fort Benton, MT	Pre: Post:	2325883 2122792	6 8,078	0.32	0.93
Wolf Point, MT	Pre: Post:	2958477 655288	6 2,136	0.62	0.25
Bismarck, ND	Pre: Post:	52788478 2791839	6 4,620	2.53	0.02
Yankton, SD	Pre: Post:	856161728 2768352	6 4,074	1.85	0.09
Omaha, NE	Pre: Post:	54295925 10052889	6 4,620	2.04	0.06
Nebraska City, NE	Pre: Post:	64983360 23629030	6 4,529	3.12	0.01
St. Joseph, MO	Pre: Post:	88501831 74308764	6 4,529	2.91	0.01
Kansas City, MO	Pre: Post:	140720000 112360000	6 4,529	2.18	0.04
Boonville, MO	Pre: Post:	191390000 189090000	6 4,802	1.58	0.15
Herman, MO	Pre: Post:	360970000 339460000	6 4,529	0.61	0.72

List of Figures

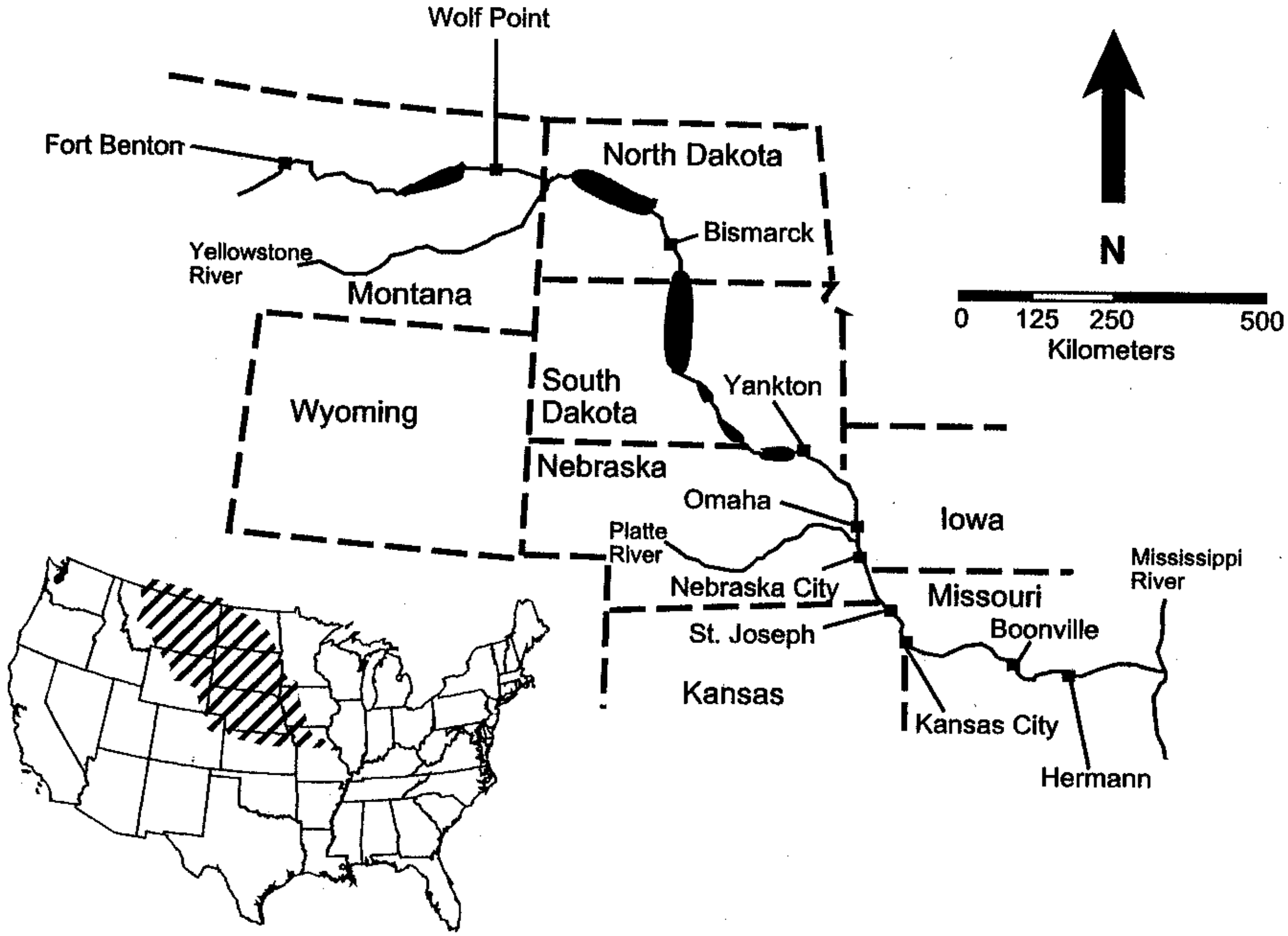

Wolf Point
Fort Benton
North Dakota
Bismarck
Yellowstone River
Montana
Wyoming
South Dakota
Yankton
Nebraska
Omaha
Iowa
Platte River
Nebraska City
Missouri
Mississippi River
St. Joseph
Boonville
Kansas
Kansas City
Hermann
N
0 125 250 500
Kilometers

Figure 1.

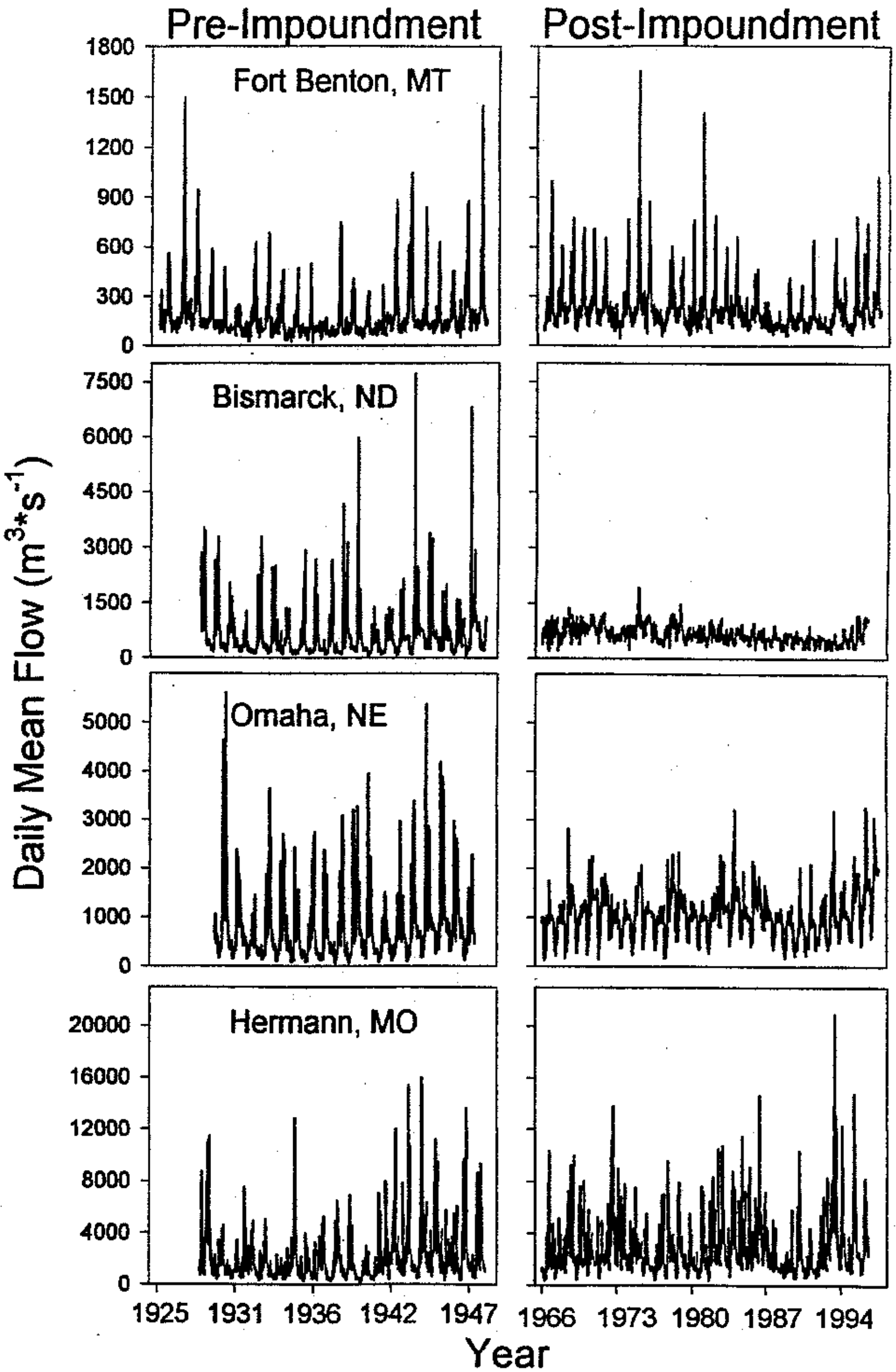
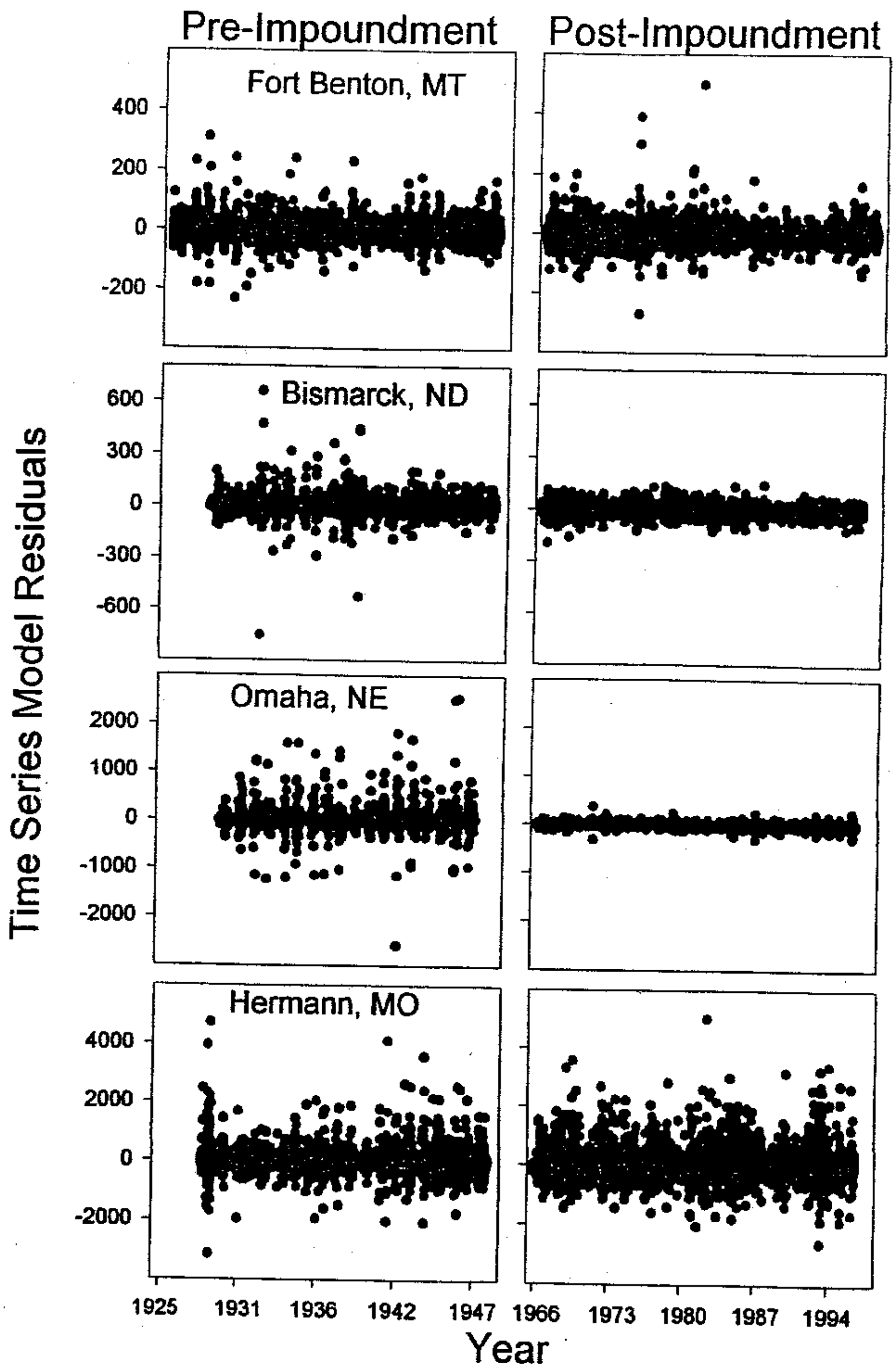
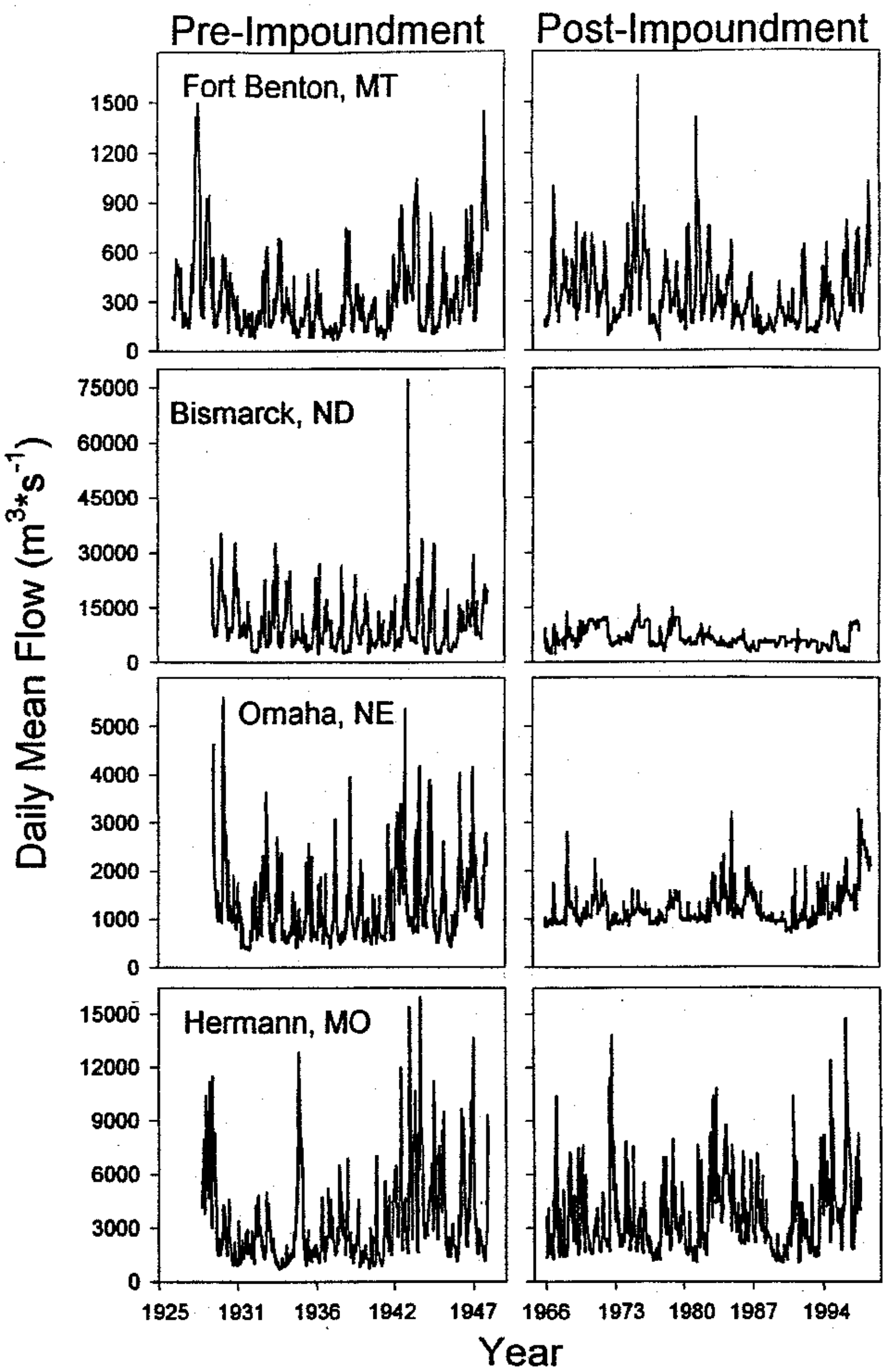

Pre-Impoundment
Post-Impoundment
Fort Benton, MT
Bismarck, ND
Omaha, NE
Hermann, MO
Daily Mean Flow (m3*s-1)
Year
1800
1500
1200
900
600
300
0
7500
6000
4500
3000
1500
0
5000
4000
3000
2000
1000
0
20000
16000
12000
8000
4000
0
1925
1931
1936
1942
1947
1966
1973
1980
1987
1994

Figure 2.



Pre-Impoundment
Post-Impoundment
Fort Benton, MT
Bismarck, ND
Omaha, NE
Hermann, MO
Time Series Model Residuals
400
200
0
-200
600
300
0
-300
-600
2000
1000
0
-1000
-2000
4000
2000
0
-2000
1925
1931
1936
1942
1947
1966
1973
1980
1987
1994
Year

Figure 3.



Pre-Impoundment
Post-Impoundment
Fort Benton, MT
Bismarck, ND
Omaha, NE
Hermann, MO
Daily Mean Flow (m^3*s^{-1})
Year
0
300
600
900
1200
1500
15000
30000
45000
60000
75000
1000
2000
3000
4000
5000
6000
9000
12000
1925
1931
1936
1942
1947
1966
1973
1980
1987
1994

Figure 4.

CHAPTER 3. CLASSIFICATION OF REACHES IN THE MISSOURI AND LOWER YELLOWSTONE RIVERS BASED ON FLOW CHARACTERISTICS

A paper to be submitted to Regulated Rivers: Research and Management

Mark A. Pegg and Clay L. Pierce

Abstract. Several aspects of flow have been shown to be important determinants of biological community structure and function in streams, yet direct application of this approach to large rivers has been limited. Using a multivariate approach, we grouped flow gauging stations into hydrologically similar reaches in the Missouri and lower Yellowstone Rivers and developed a model based on flow variability parameters that could be used to test hypotheses about the role of flow in determining community structure, and for future comparisons as the hydrological regime changes. Forty hydrological parameters for the recent, post-impoundment period (1 October 1966 through 30 September 1996) for each of 15 gauging stations along the Missouri and lower Yellowstone Rivers were initially used. Preliminary graphical exploration identified six variables for use in further multivariate analyses. Six hydrologically distinct units composed of gauge stations exhibiting similar flow characteristics were then identified using cluster analysis. Discriminant analyses identified the four most influential variables as: flow per unit drainage area, coefficient of variation of mean annual flow, flow predictability, and flow constancy. A classification tree model further supported the findings of the cluster analysis and provides a predictive tool to forecast effects

of future changes in reservoir water release schedules. One surprising result was the relative similarity of flow regimes between the two uppermost and three lowermost gauge stations, despite large differences in magnitude of flow and separation by roughly 3000 km. Our results synthesize, simplify, and interpret the complex changes in flow occurring along the Missouri and lower Yellowstone Rivers, and provide an objective grouping of portions of the river for future tests of how these changes affect biological communities.

Introduction

Management of flow in regulated rivers and streams typically focuses on maintaining maximum, minimum, and mean flows in direct response to flood control, navigation, hydropower generation, irrigation, and other human needs (Poff et al. 1997). However, when evaluating the responses of biological communities to differences in flow, it may be necessary to take a more refined approach to analyzing hydrological data (Church 1995). Several stream flow variables have been used to describe the physical environment of streams and how organisms respond to these factors (Statzner and Higler 1986; Bain et al. 1988; Schlosser 1985; Poff and Ward 1989; Poff 1992; Townsend and Hildrew 1994). Indeed, several studies have reported that hydrological factors, specifically flow variability, can influence aquatic community structure (Horwitz 1978; Coon 1987; Bain et al. 1988; Fausch and Bramblett 1991; DiMaio and Corkum 1995; Poff and Allan 1995). This variability can occur at different temporal scales (e.g. seasonally or annually; Townsend and Hildrew 1994).

Because of the many ways that the magnitude and variability of flow can be characterized (Poff and Ward 1989), analyzing flow variables using a multivariate approach is an effective means to determine similarities or differences among and/or within lotic systems. Hydrologically similar reaches can be classified into groups. The resulting classification system can then be used as a basis for testing whether hydrology influences the biological community among the groups. When relating characteristics of the biological community to hydrological conditions, it is necessary that these groupings are objectively determined and made *a priori* to assessment.

Most of the previous studies characterizing and grouping lotic reaches by flow regime have focused primarily on small order streams. Poff and Ward (1989) characterized and classified 78 streams (mean annual flows < 30 $m^3 \cdot s^{-1}$) located across the United States using a suite of variables calculated from daily and peak flow values for each stream. They speculated on the biological significance of these different hydrological regimes, and Poff and Allan (1995) subsequently confirmed several predictions for fish communities in small and medium sized streams.

Classification of reaches exhibiting similar hydrological conditions within a system also has potential (Richter et al. 1998). This may be especially important in assessing hydrological conditions in larger rivers, which are limited in number but may exhibit great variation in flow conditions from headwaters to mouth. Many large rivers, such as the Missouri, have undergone modification to support human needs (e.g., impoundment and channelization) that can influence flow characteristics (Nilsson et al. 1991; Hesse and Mestl 1993; Poff et al. 1997; Parasiewicz et al. 1998; Pegg, unpublished data). The result could potentially be several unique hydrological areas within one large river system. Furthermore, many of these changes may not necessarily be simple, linear functions of the longitudinal increase in drainage area and discharge.

The Missouri River is the longest river in the United States stretching nearly 4,400 km from western Montana to its confluence with the Mississippi River in Missouri (Figure 1). In addition to its great length, the Missouri River system also drains about one-sixth of the total area of the United States (Berner 1951). Prior to channelization and impoundment in the early to mid 1900's, the Missouri River was characterized as a meandering, turbid river laden with islands (Funk and Robinson 1974). After channelization, however, the Missouri below Sioux City, Iowa was changed into a fairly narrow and swift flowing river, resulting in a shortening of the channel by 125 km and reduction of the wetted area by nearly 64% (Whitley and Campbell 1974). Likewise, the construction of six major reservoirs in the middle portion of the river has also changed water quality above and below the dams (Morris et al. 1968) and altered the hydrology of major portions of the river (Hesse and Mestl 1993). These major alterations have essentially divided the Missouri River into three zones, an upper zone upstream from the major alterations, a middle zone with short free-flowing reaches between reservoirs, and a lower channelized zone.

Objectives of this study were to, first, identify hydrologically similar reaches from the Missouri and lower Yellowstone Rivers using a suite of variables calculated from daily mean flow values. The second objective was to create an easily interpreted model of the important flow variables used in the classification process. These results will provide an objective grouping of portions of the river for future tests of how these differences affect biological communities. Future changes imposed on the Missouri River hydrology could also be assessed using the groupings identified in this study.

Methods

Long-term discharge records are available for several gauging stations along the mainstem Missouri and lower Yellowstone Rivers from the United States Geological Survey (USGS) via electronic media. These gauging stations yield a point measure for a given reach, providing insight into the general conditions within that portion of river. For purposes of this study, we used the 15 gauge stations (Figure 1) with complete flow data from water year (October - September) 1967 through 1996. These dates define the years after closure of the impoundments along the mainstem Missouri River and therefore reflect the current, post-impoundment hydrological regime (Galat and Lipkin 2000; Pegg, unpublished data). We included a site on the lower Yellowstone River (Sydney, MT) because it is a large tributary (discharge greater than the Missouri River at their confluence) that has undergone a limited amount of alteration (Benke 1990). Thus, in terms of flow alteration, the lower Yellowstone is similar to the Missouri River above Fort Peck Reservoir (Figure 1). Inclusion of this site provided further information from relatively pristine areas for comparisons of flow variability with the more heavily human influenced downstream areas of the Missouri River. We did not use stations located within the water storage areas of impoundments because we wanted to focus solely on riverine flow variability.

A suite of 40 hydrological variables were calculated for each gauge station from mean daily flow data using the Indicators of Hydrologic Alteration (IHA) methodology (Richter et al. 1996). Resulting data from the IHA calculations were reported by Galat and Lipkin (2000) for eleven of the fifteen gauging stations reported here. We calculated the IHA variables for the remaining stations using the IHA software (The Nature Conservancy 1997). This suite of variables provides information on the flow conditions (e.g. variability, predictability, magnitude) at each gauging station over the period of record. The IHA method places each of these variables into one of five categories: 1) monthly flows, which focuses on the mean monthly flows; 2) magnitude and duration of extremes, giving insight into the extent and duration of both high and low flow extremes; 3) time of extreme events, giving the mean date of the extreme events; 4) characteristics of flow pulses, providing information on the number and length of flow extremes; and 5) rate of change, which gives the rate and mean number of changes in flow conditions (e.g., rising or falling) from day to day (Richter et al 1996).

The large number of variables calculated for a relatively small number of gauge stations precluded immediate application of some common multivariate procedures. Therefore, we used a high dimensional, graphical data exploration program (XGobi) to identify a subsample of the descriptive variables that could be useful in further analyses (Swayne et al. 1998). XGobi allows projection of an *n*-dimensional plot in a series of linked, 2-dimensional plots, and interpretation of patterns within the data is facilitated by the ability to view more than one plane of the diagram by rotating the multiple variable plots. Simultaneous visualization of several variables in this format can thus provide insight into which variables may be meaningful in further analyses.

Multivariate analysis of the IHA variables followed two steps. In the first step, we grouped gauging stations that exhibited similar flow characteristics. We used cluster analysis to determine the centroid distance for all gauge stations with the variables identified in the data exploration stage (SAS 1987). We then determined meaningful cluster breaks using a minimum threshold criterion from the distance between two clusters (Sharma 1996). Cluster distances greater than the threshold were considered to indicate distinct clusters. We then placed stations most closely linked, and considered to be relatively homogenous, into common flow variability units.

The second step determined which variables accounted for the most variation among these units. We used stepwise discriminant analysis to identify which variables best discriminated among the groupings from the cluster analysis. Once these variables were determined, we used discriminant analysis to determine the classification error rate. Determination of classification rates provides insight into the validity of groups based upon the empirical data used in defining the groups (Sharma 1996).

Finally, we developed a classification tree model to supplement the preceding multivariate techniques using the S-PLUS programming environment (Venables and Ripley 1994). Classification trees can be viewed as a type of variable selection where concerns of interaction among variables are automatically handled (Venables and Ripley 1994). These trees describe responses to dependent groups based on several independent variables similar to multiple regression methods. However, the classification tree method uses a hierarchy of predictions to classify to which group the dependent variable should belong (StatSoft 1999). This can result in several predictions for one observation, whereas multiple regression methods make only one prediction for each case. An important benefit of this technique is that the resulting tree is relatively easy to understand and interpret (Breiman et al. 1984).

Results

Fourteen stations from the Missouri River and one Yellowstone River station were used to identify the flow variability units (Figure 1). Of those 15 stations, IHA data were available for 11 in Galat and Lipkin (2000). We calculated IHA variables for the remaining stations located at Virgelle, Fort Peck, and Culbertson, Montana, and Sioux City, Iowa (Figure 1).

Graphical exploration of the IHA variables indicated that several could be useful for clustering the 15 gauging stations into units. However, nearly all of the variables that specifically dealt with central tendencies of the flow values (e.g. mean annual flow, mean monthly flow, median monthly flow, etc.) were strongly correlated with watershed size. Furthermore, the location of gauging stations in longitudinal sequence along the Missouri River resulted in pronounced serial autocorrelation among these variables. Hence, we used only variables that were not directly influenced by watershed size (increasing trend moving downstream) to group the gauging stations. Graphical exploration of this subset of the data indicated that six variables could be used to identify hydrologically different reaches of the Missouri and lower Yellowstone Rivers. Flow per unit drainage area (FPA) is the ratio of daily mean discharge at the gauge station to the watershed area above the gauge over all years. Coefficient of variation for mean annual flow (FCV) is a dimensionless parameter that represents the ratio of standard deviation of the mean daily flow to its mean. Flow predictability (FP) is the measure of variation among successive periods (Colwell 1974) and ranges from zero to one, where high predictability values indicate low variability. Predictability is comprised of two components which were also included in the cluster analysis: flow contingency (FCTG) and flow constancy (FC). Flow contingency is a measure of periodicity meaning that flows can vary quite dramatically yet still have a high FP score if similar flows occur at a consistent periodicity. Conversely, relatively stable flows would also have high predictability, but the major component would be constancy rather than contingency. The final variable we identified in the graphical exploration stage was the ratio of FC to FP (CP), which gives the magnitude of the consistency component used to calculate FP. See Colwell (1974) and Poff and Ward (1989) for further explanation and rationale of these variables.

In contrast to the steady increase in annual mean discharge, there was no evidence of continuous longitudinal trends throughout the entire length of the Missouri River in any of the flow variables we analyzed (Figure 2). However, there were continuous trends evident over considerable lengths of the uppermost and lowermost portions of the river for several variables. FPA declined steadily in the upper section and decreased steadily in the lower section. FP and FC declined steadily in the lower section. FCV in the lower portion of the river exhibited a sigmoid pattern, with low values for the first four stations below the lowest reservoir, followed by a sharp increase over the next three stations, finally stabilizing in the lower section (Figure 2).

In addition to separating portions of the river where continuous flow trends occurred, the mainstem reservoirs also corresponded with other flow discontinuities (Figures 1, 2). On the Missouri River, FCV decreased dramatically between the stations directly above and below Ft. Peck Reservoir, increased dramatically between Wolf Point and Culbertson, and decreased dramatically again between Culbertson and Bismarck. The decline in FCV between Sydney on the lower Yellowstone River and Bismarck was very similar to the decline between Culbertson and Bismarck. However, the Sydney station, which is similar to the Ft. Benton and Virgelle stations on the Missouri in that it is unaffected by large mainstem reservoirs, had distinctly lower values for FC and CP than Missouri stations both above and below Ft. Peck Reservoir (Figures 1, 2).

We identified six hydrologically distinct units from the cluster analysis: (1) Inter-reservoir I (IR-I); (2) Upper Channelized (UU); (3) Lower Channelized (LC); (4) Upper Unchannelized (UU); (5) Inter-reservoir II (IR-II); and (6) Unchannelized Yellowstone (UYS; Figure 3). Stations often clustered more closely with distant than adjacent stations (Figure 2, 3). Interestingly, although they include the most spatially distant stations, the UU and LC units clustered closer to each other than to units consisting of nearby stations.

Stepwise discriminant analysis indicated that four of the original six variables significantly contributed to clustering the stations into similar hydrological units (Figure 2). Univariate F-tests identified the contributing variables as FCV (F= 41.2; P = 0.0001), FPA (F= 15.25; P = 0.0007); FP (F= 6.92; P = 0.012), and FC (F = 4.2; P= 0.05). Discriminant analysis correctly classified all 15 stations into their appropriate unit based on these four variables. Pairwise correlations among these four variables were generally low and not statistically significant (P > 0.05).

The UU, IR-II, and UYS units were characterized as having higher values for the four influential variables identified in the discriminant analysis (Figure 2). The UC unit had the overall lowest values; whereas, the IR-I and LC unit values were somewhat intermediate.

The classification tree model (Figure 4) also had a 100% correct classification rate. The four influential variables identified by discriminant analysis were included in the development of this tree. However, FPA and FCV appeared to have the greatest effect in classification of the hydrological units within the model. Therefore, the resulting model used only these two variables to correctly classify all six flow variability units.

Discussion

The grouping of gauge stations into six flow variability units by our analyses generally followed a longitudinal continuum along the river system. This makes intuitive sense due to the cumulative nature of flow along the river's course. However, the division of the river into discrete units begs the questions of where and why these unit breaks occur. There are two likely reasons for the majority of the unit differences. The first is the fact that the Missouri River has essentially been divided into three parts due to the massive alterations to the river during the early to mid 1900's. Impoundments and channelization in the middle and lower river have effectively divided the river into an upper least-altered area, a middle inter-reservoir area, and a lower channelized area. These management practices have had a strong influence on the channel morphology and hydrology of the middle and lower Missouri River (Hesse and Mestl 1993; Galat and Lipkin 2000). So, this allows the first, coarse step in a logical division of the major sections of the river. However, our detailed analysis of flow variability suggests further subdivision within these broad areas.

Flow patterns not intuitively linked with river alteration were also evident from our analyses. The UU unit is characterized as having the highest FPA values in all the stations we studied (Figure 2). The coefficient of flow variation (FCV) and FP tended to be relatively high in this unit as well. The high FCV score indicates a relatively large amount of annual flow variability within this unit, but high FP indicates that this variability does occur with relatively regular periodicity.

The IR-I unit had the lowest amount of variation (FCV) and relatively high predictability when compared to the other units (Figure 2). Flow constancy was also high which played a large role in classifying this unit. Flow variability immediately downstream of dams tends to be reduced (Ligon et al. 1995). Thus, constancy is a consequence of the close downstream proximity of the gauge stations to dams in the IR-I unit. The result is stable flow throughout the recent, post-regulation period of record.

The IR-II unit was similar to Inter-reservoir I except that FCV was markedly higher. The higher annual variation is most likely due to the input from tributaries. Between the Wolf Point and Culbertson gauge stations (Figure 1), two tributaries (Poplar River and Big Muddy Creek) enter the Missouri River. Streams in this region tend to be quite variable and dependent upon snowmelt in the spring and unpredictable precipitation throughout the remainder of the year (Poff and Ward 1989). These tributaries typically contribute 1-2% of the mean annual flow to the Missouri River at the Culbertson gauge. However, during high precipitation periods, the tributaries can contribute as much as 5 - 15% to the total flow. It would follow then, that the tributaries joining the Missouri would add flow variability to this unit during these high flow periods. The added variability has created a point of separation between the two inter-reservoir units.

Similar to the IR-II unit, the UYS also had a high FCV value in addition to the lowest FC and CP of all the stations. This would indicate that, while predictability is fairly similar to the other units, there is a large amount of annual variation. Consequently, the lower consistency suggests that there is a fair amount of daily and monthly variability, albeit occurring with some regularity, which can be attributed to its relatively free-flowing nature (Benke 1990). This conclusion is also supported by Galat and Lipkin (2000) who reported the lower Yellowstone River to be the least hydrologically altered reach of the Missouri and lower Yellowstone Rivers. Thus, flows in the UYS unit tend to be more variable than the units of the Missouri River due to this natural heterogeneity.

Located directly below the six mainstem reservoirs and in the upstream portion of the channelized navigation corridor, the UC unit is in a unique position on the Missouri River (Figure 2). The regulated flows coming out of the inter-reservoir units and reservoirs resulted in the lowest FCV values of any in the system. Additionally, there are few major tributaries that could contribute additional flow. The one exception to this is the Platte River which provides about 8% of the mean annual flow at Hermann, MO (the lowermost gauge station on the Missouri River). The low FPA scores reflect this lack of tributary contribution as it remains fairly low throughout this unit (Figure 2). The classification tree (Figure 4) also uses FPA as the major criterion for separating the UC unit from the other units. The combination of upstream influence from the impoundments and the scarcity of major tributaries results in one of the more stable flow units.

Finally, the LC unit exhibits more variability than the UC unit as the Missouri River approaches the confluence with the Mississippi River. Geographically, this units watershed area drains about 38% of the entire Missouri River basin, but supplies 61% of the average annual flow to the system (Galat and Lipkin 2000). Additionally, the major tributaries within the LC unit (e.g., Kansas River, Grand River, Osage River) contribute nearly half (44%) of the total annual flows at Hermann, Mo. Input from these tributaries ameliorates some of the influence that the impoundments have on the middle portion of the river, resulting in much higher FPA values compared to the UC unit. Flow predictability also reaches some of the lowest values (Figure 2) reflecting the renewed variability within the system. The result is a relatively variable unit, giving the flows in this area a less regulated characteristic.

A consequence of this renewed variability, revealed by the cluster analysis, is the linkage between the extreme upstream and downstream units. The cluster analysis dendrogram (Figure 3) shows that the UC and LC units are more closely related with each other than with any of the other units. Galat and Lipkin (2000) reported similar results from their analysis with lower levels of alteration in the extreme upstream and downstream reaches of the Missouri River. Again, this is probably attributable to the input of the larger tributaries found in the LC unit which mediate the effects of impoundment and channelization felt in the middle part of the river.

The hydrological effects of reservoirs are most notably observed on flow variations within a year (Allan 1995; Hesse and Mestl 1993). Specifically, mainstem Missouri River impoundments have typically been thought to change the timing rather than total discharge by depressing maximum flows and raising minimum flows throughout the year (Hesse and Mestl 1993). Each reservoir has specific operating requirements that mandate particular water levels at certain times of year (USACOE 1998). There are exceptions to this (i.e., some filling takes place in wet years that were preceded by dry years), but generally the same amount of water flowing into a reservoir flows out. If the total amount of discharge does not change over the length of the reservoirs, then our FCV estimates should reflect similar values at each station along the river because they are calculated at the inter-annual scale. Figure 2 indicates that this is not the case as variability in the inter-reservoir units is markedly lower than the other units. This suggests that the inter-annual effects from reservoirs may be greater than previously thought and warrants further investigation.

Our approach has identified six hydrologically distinct units along the Missouri and lower Yellowstone river system based on inter-annual patterns in flow variability. An important utility of this classification will be in future testing for responses of lotic organisms to the differing flow conditions occurring in these units. Studies investigating among-stream differences at the intra-annual scale have shown that flow characteristics can influence the composition and structure of biological communities (Horwitz 1978; Coon 1987; Bain et al. 1988; Fausch and Bramblett 1991; DiMaio and Corkum 1995; Poff and Allan 1995). For fish, the basic premise is that assemblages in hydrologically stable environments tend to consist primarily of species with specialized life histories. Conversely, highly variable conditions are more conducive to generalist life history traits. Application of this theory at the inter-annual temporal scale and to larger rivers has been limited due to the lack of multiple systems with similar characteristics for hypothesis testing. Comparing community attributes within one large system is especially difficult because of the inherent longitudinal zonation of species richness and diversity (Statzner and Higler 1986), and perhaps further complicated by the disruptive nature of impoundments upon this gradient (Ward and Stanford 1995). We expect the LC unit to have the highest aquatic species diversity due to both its position in the drainage network, lack of barriers to upstream migration from downstream source populations, and the less regulated nature of the flows. Conversely, the inter-reservoir units would be expected to have lower diversity estimates due to the influence of the reservoirs, position between physical barriers, and longitudinal position. The next step will be to test these predictions using biological data from the Missouri and lower Yellowstone Rivers. We are currently addressing some of these questions, along with a collaborating group of researchers (Young et al. 1997).

The classification tree (Figure 4) developed here would be useful for examining changes in the flow of the Missouri River system if water release schedules were to change. Unlike other multivariate methods, classification trees use the actual variable values to classify branches. The underlying processes used to develop this tree were complex, but the resulting tree is fairly simple to understand (Breiman 1984), facilitating its use in future decision making processes. For example, if the hydrograph were changed, as has been proposed by Hesse and Mestl (1993) or the U.S. Army Corp of Engineers (USACOE 1998), estimates of these changes in the tree variables could yield predictions regarding how flow regimes might shift in various portions of the river.

In large systems such as the Missouri River, there are reasons to group river reaches in various ways to meet specific goals. The division of the river into three parts defined by human alteration, discussed earlier, is a useful first step in identifying regions sharing basic characteristics. Dividing the river by other criteria (e.g., political, climatic, topographical) might also have utility for certain uses. However, we believe that by objectively creating groups based on a suite of driving variables with demonstrated biological significance as we have done here, we can set the stage for further exploration into how these factors influence biological communities in large river systems.

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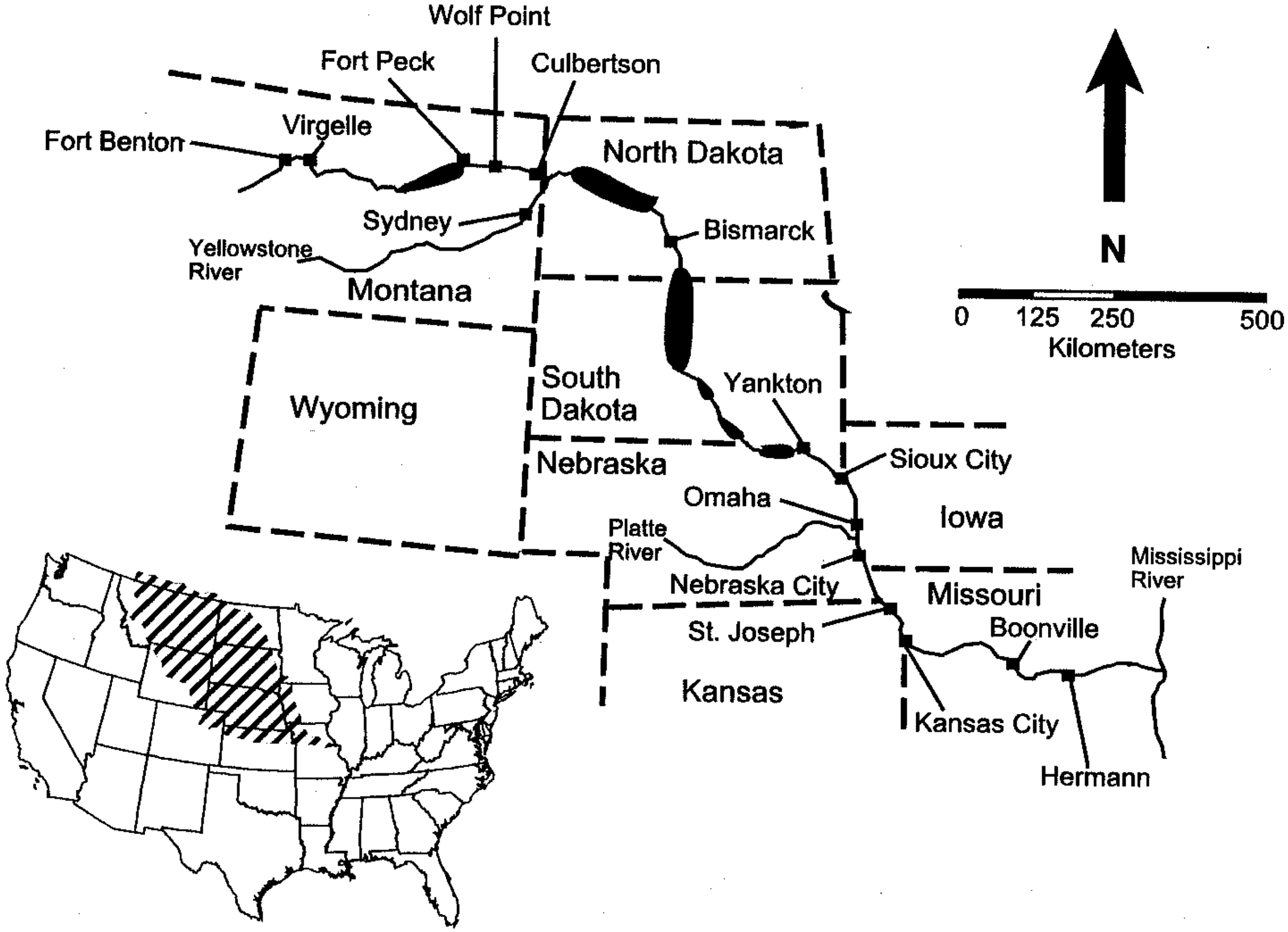
List of Figures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250
500
Kilometers
Wyoming
South
Dakota
Yankton
Nebraska
Sioux City
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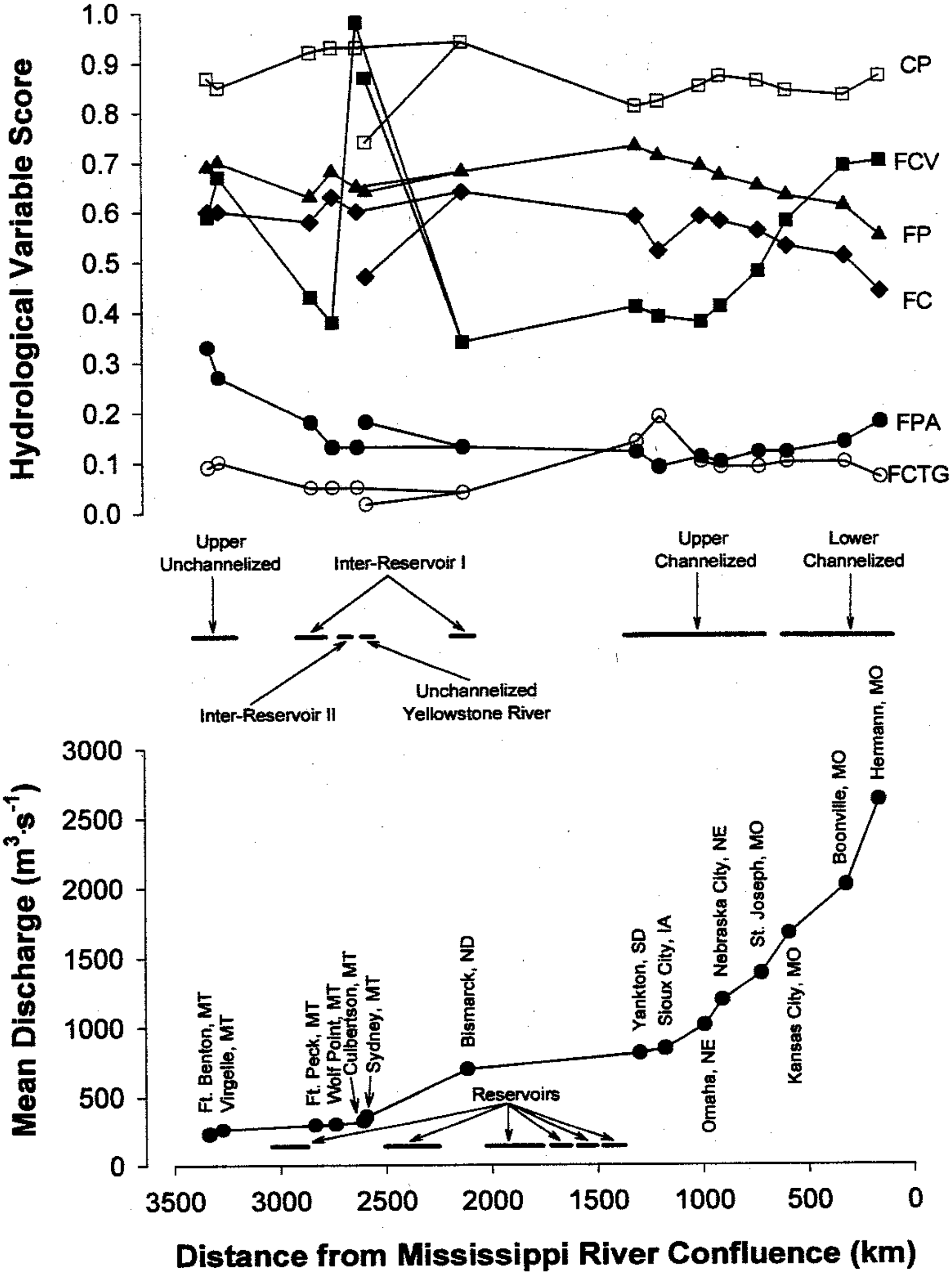
Hermann

Figure 1.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CP
FCV
FP
FC
FPA
FCTG
Upper Unchannelized
Inter-Reservoir I
Upper Channelized
Lower Channelized
Inter-Reservoir II
Unchannelized Yellowstone River
Mean Discharge ($m^3 \cdot s^{-1}$)
3000
2500
2000
1500
1000
500
0
Ft. Benton, MT
Virgelle, MT
Ft. Peck, MT
Wolf Point, MT
Culbertson, MT
Sydney, MT
Bismarck, ND
Yankton, SD
Sioux City, IA
Omaha, NE
Nebraska City, NE
St. Joseph, MO
Kansas City, MO
Boonville, MO
Hermann, MO
Reservoirs
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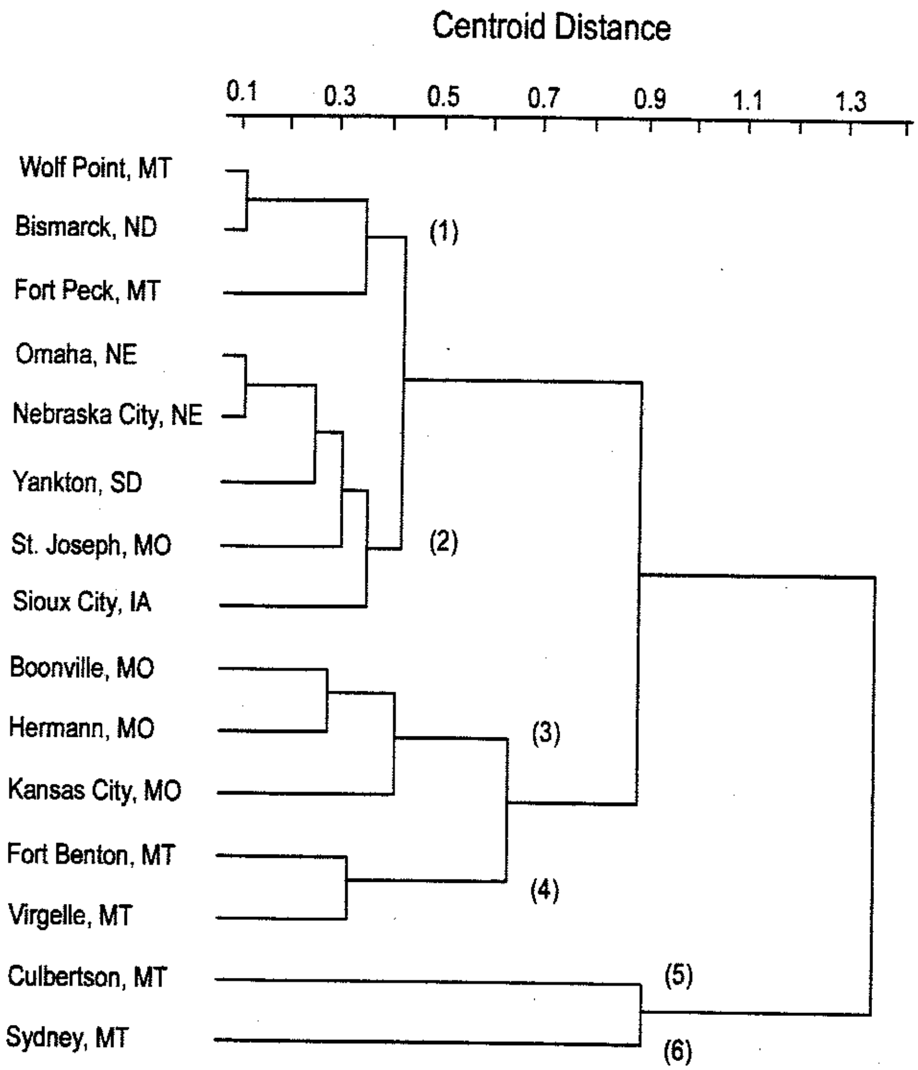
3000
2500
2000
1500
1000
500
0
Distance from Mississippi River Confluence (km)

Figure 2.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Omaha, NE
Nebraska City, NE
Yankton, SD
St. Joseph, MO
Sioux City, IA
Boonville, MO
Hermann, MO
Kansas City, MO
Fort Benton, MT
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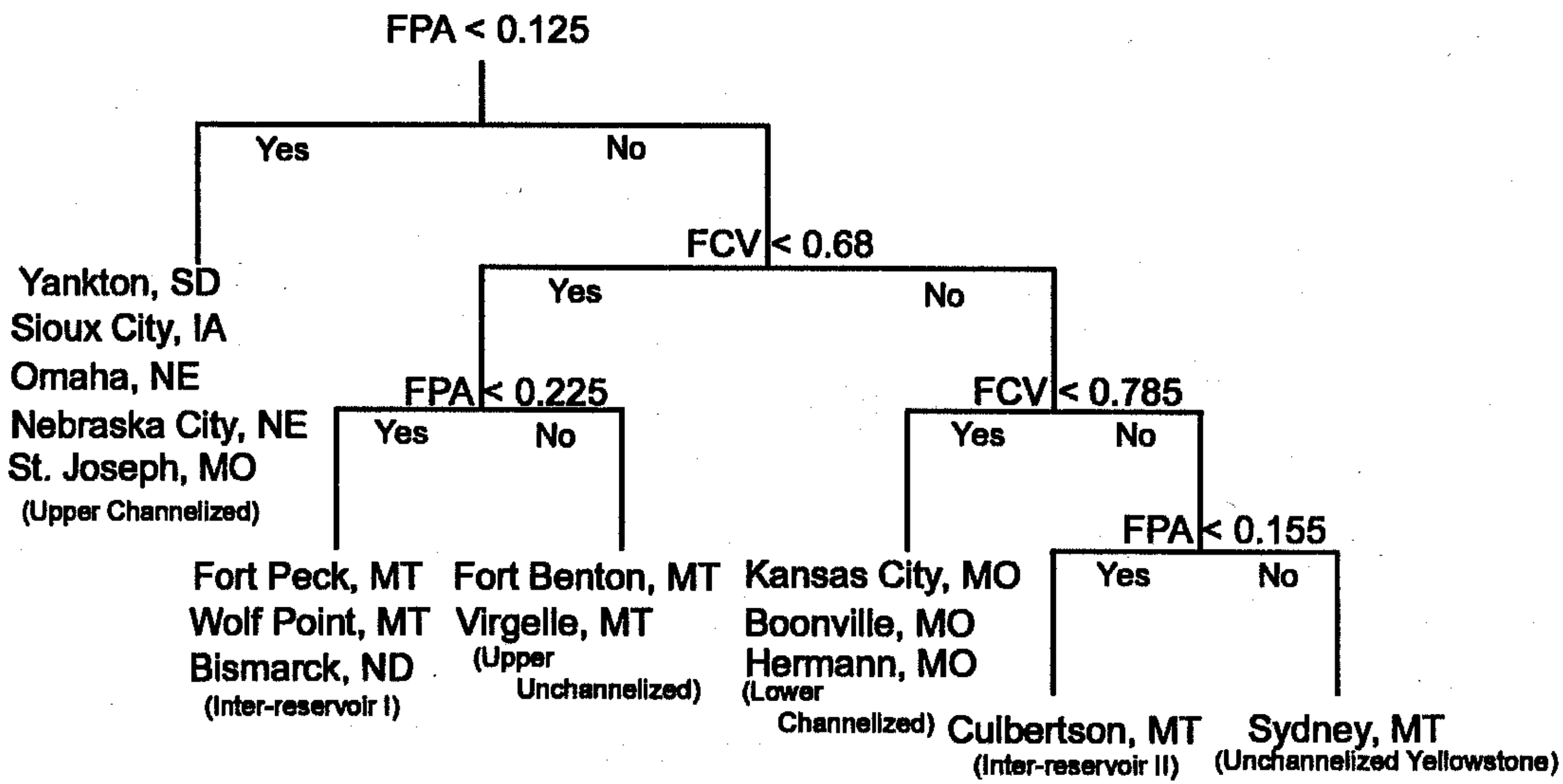
Sydney, MT
(1)
(2)
(3)
(4)
(5)
(6)

Figure 3.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No
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Sioux City, IA
Omaha, NE
Nebraska City, NE
St. Joseph, MO
(Upper Channelized)
FCV < 0.68
Yes
No
FPA < 0.225
Yes
No
Fort Peck, MT
Wolf Point, MT
Bismarck, ND
(Inter-reservoir I)
Fort Benton, MT
Virgelle, MT
(Upper Unchannelized)
FCV < 0.785
Yes
No
Kansas City, MO
Boonville, MO
Hermann, MO
(Lower Channelized)
FPA < 0.155
Yes
No
Culbertson, MT
(Inter-reservoir II)
Sydney, MT
(Unchannelized Yellowstone)

Figure 4.

CHAPTER 4. FISH COMMUNITY STRUCTURE IN THE MISSOURI AND LOWER YELLOWSTONE RIVERS IN RELATION TO FLOW CHARACTERISTICS

A paper to be submitted to Ecological Applications

Mark A. Pegg and Clay L. Pierce

Abstract. Human alteration is commonplace among large rivers and often results in changes in the flow regime which can lead to changes in fish community structure. We explored the characteristics of fish community structure, morphological characteristics, functional composition, and life-history attributes in relation to six unique flow regimes in the Missouri and lower Yellowstone Rivers. We found significant differences ($P < 0.01$) in community composition and abundance. The clearest pattern in our results was the distinction between the channelized portion of the river below the mainstem reservoirs from all other parts of the Missouri and lower Yellowstone Rivers due to a marked reduction of species richness above the reservoirs. We also found morphological, functional, and life-history differences ($P < 0.05$) among the flow units, with the inter-reservoir communities consisting of slightly more generalist characteristics. Our results suggest some relation between flow and fish community structure, but that human alteration may have the strongest influence in distinguishing community differences in the Missouri and lower Yellowstone Rivers.

Introduction

Human alteration has had an extensive influence on the ecology of large rivers by changing the structure and function of aquatic communities. Changes in water quality, habitat quality and nutrient cycling are factors generally associated with human activity (Karr et al. 1986). Flow regimes are also changed by controlling water via impoundments, channelization, or other flow entrainment structures. These management practices are directed toward flood control and/or maintaining a reliable source of water for navigation, hydropower, irrigation, and consumptive uses that can influence biotic communities by maintaining unnatural conditions.

Many flow variables have been used to describe the physical environment of streams including flow stability, predictability and variability (Statzner and Higler 1986; Bain et al. 1988; Schlosser 1985; Poff and Ward 1989; Poff 1992; Townsend and Hildrew 1994) and have shown that these variables do influence community structure of aquatic organisms. Poff and Allan (1995) also used several flow variables as a predictive tool to describe fish communities in small streams. Prediction of fish assemblages using physical characteristics, specifically flow, stem from refinements of Southwood's (1977) habitat templet. The basic premise is that fish assemblages in stable environments will support specialist species that rely upon stable resources. This assemblage will usually consist of both long and short lived species (Townsend and Hildrew 1994). Conversely, highly variable environments will support a more opportunistic fish assemblage that can take advantage of resources as they become available (Poff 1992; Townsend and Hildrew 1994; Poff and Allan 1995).

Assemblages in highly variable environments will typically be dominated by species that exhibit generalist characteristics.

Variability and stability in lotic systems are typically defined by the frequency, timing, and magnitude of changes between high and low flows. This does not mean every flood or drought will influence a species assemblage. Many species have evolved to exploit spring flooding in rivers (Junk et al. 1989) so a clear distinction between the ecological and evolutionary time scale of flow disturbances which influence species assemblages is needed (Poff 1992). When a natural disturbance is relatively predictable (e.g., spring floods), little change in community structure will occur because the community has evolved with this phenomenon. Less predictable ecological disturbances immediately change habitat availability which can cause shifts in the species assemblage. In other words, if flooding episodes have low predictability in a river or stream, then the event is more likely to act as an ecological disturbance which favors generalist species. This theory then provides a basis from which to test for differences of fish assemblages based on hydrological parameters. Poff and Ward (1989) established the basis for this type of assessment by classifying 78 streams from the United States into nine categories exhibiting different flow regimes. Poff and Allan (1995) found that hydrologic factors influenced fish community structure supporting several earlier predictions (Poff and Ward 1989). Likewise, DiMaio and Corkum (1995) identified distinct freshwater Unionid assemblages associated with different hydrologic regimes in Great Lakes tributaries.

Most of the research on linking flow characteristics to fish community structure has been conducted on small streams because they are ubiquitous and easier to sample than larger rivers. The difficulty in collecting data from large rivers has been a limitation, but as restoration and mitigation efforts increase, there is urgent need to gain an understanding of how aquatic communities are influenced by human alteration. One effect of this alteration on the Missouri River is a change in flow characteristics (Chapter 2; Galat and Lipkin 2000). Pegg and Pierce (Chapter 3), Pegg et al. (Chapter 2) and Galat and Lipkin (2000) reported a large amount of flow variability in the Missouri River due to its large expanse and history of alteration. This variability has resulted in regions differing in a suite of flow characteristics which, in turn, may influence the fish community.

The purpose of this study was to explore characteristics of fish community structure, functional composition, and life-history attributes in relation to flow regimes in the Missouri and lower Yellowstone Rivers. Our specific objectives were to 1) characterize the species richness and composition, functional composition, and proportional life-history composition of portions of these rivers differing in flow characteristics, 2) test for differences in fish communities among portions of the river differing in flow characteristics, 3) examine the pattern of responses in relation to flow regimes associated with human alteration, and 4) test the hypothesis that fish communities in areas with altered flow regimes exhibit more generalist functional and life-history characteristics than communities from unaltered areas.

Methods

Fish Community and Flow Data

We collected fish from 15 segments located throughout the riverine portions of the Missouri and lower Yellowstone Rivers during the late summer and early fall of 1996-1998.

The goals of our sampling design were to qualitatively and quantitatively characterize the fish communities throughout the river system, and to enable river-wide comparisons among segments differing in flow, habitat, and other characteristics. Within each segment, six macrohabitat types were sampled, including inside and outside bend, main channel at the cross-over point between bends, tributary mouth, connected side channel, and unconnected side channel. Sampling gears used included boat electrofisher, beam trawl, bag seine, stationary gill net, and drifted trammel net, and two of these gears were used in each macrohabitat. We attempted to sample five replicates of each macrohabitat type in each segment, although there were minor differences in the number of samples taken among segments due to differing availability of some macrohabitats, especially side channels and tributary mouths. For this analysis, we adjusted catches to our *a priori* standardized sampling effort within segments. Complete details and rationale for sampling design, sampling procedures, data processing, and quality assurance are reported in Sappington et al. (1998).

We related fish community characteristics to differing flow regimes previously identified in the Missouri and lower Yellowstone Rivers (Chapter 3). Using daily mean flow data from 15 gauge stations during the recent, post-alteration period (1996-1996) six distinct flow units exhibiting differing combinations of flow variability and predictability were identified. Flow units include Upper Unchannelized (UU), Unchannelized Yellowstone (UYS), Inter-Reservoir I (IR-I), Inter-Reservoir II (IR-II), Upper Channelized (UC), and Lower Channelized (LC) (Figure 1). The number of segments for fish sampling located within flow units ranged from one to four, so the number of segments per unit was used in the analysis to adjust for an unequal number of segments, and thus fish sampling effort within flow units.

Data Analysis

Differences in community structure among the flow units were determined with multidimensional scaling ordination (MDS) of the species abundance (adjusted total catch) data using a Bray-Curtis similarity matrix. Double square-root transformations were used to moderate the dominance of extreme abundances. The resulting Bray-Curtis matrix provided only one data point for each unit and year combination. Therefore, we evaluated the significance of these differences using a two-way crossed Analysis of Similarity (ANOSIM2) with no replication (Warwick et al. 1990; Clarke and Warwick 1994a; 1994b).

We investigated morphological, functional, and life-history characteristics of fish communities within and among the six hydrologic units. Most of the data for these analyses were previously compiled by Winemiller and Rose (1992) and Poff and Allan (1995). Data were not previously summarized for some species, so we compiled them from various sources and classified them following Winemiller and Rose (1992) and Poff and Allan (1995). Descriptions of these characteristics are shown in Table 1.

Most variables listed in Table 1 are self-evident and have been adequately defined elsewhere (Winemiller and Rose 1992). However, three lesser known variables are shape factor, swim factor and parental care. Shape factor is the ratio of total length to maximum body depth. A high ratio indicates a more elongate body shape which implies better swimming ability in swift current. Swim factor is the ratio of the minimum depth of the caudal peduncle to maximum depth of the caudal fin. Low ratios imply capability of strong, prolonged swimming (Poff and Allan 1995). Parental care is the sum of three scores (placement of zygotes, protection of zygotes or larvae, nutritional contribution) and can range from no care (0) to large amount of energy put into care (8).

We tested for life-history differences among units by weighting each morphological, functional, and life-history characteristic value by the adjusted catch for each species and unit combination. The overall score for each unit was the average scores for all species present in the unit, weighted by their relative abundance. We then used analysis of variance (ANOVA) for continuous variables and a Kruskal-Wallis test for categorical variables to determine differences among units.

Results

Our MDS analysis of Bray-Curtis similarities indicate differences in fish community structure and abundance among the six flow units (Figure 2). Dimension 1 clearly separates the channelized units from all other units, and also provided some separation between the UC and LC units. We found strong negative correlations ($P \leq 0.05$) of species abundances for channel catfish Ictalurus punctatus, emerald shiner Notropis atherinoides, freshwater drum Aplodinotus grunniens, and longnose dace Rhynichthys cataractae and a positive correlation for fathead minnow Pimphales promelas abundances with dimension 1 (Table 2; Figure 2). Species abundances for flathead chub Platygobio gracilis and longnose dace were negatively correlated to dimension 2, while correlations for river shiner Notropis blennius abundances and dimension 2 were positive.

We also found a strong negative correlation ($r = -0.95$; $P < 0.01$) of species richness to dimension 1 suggesting that these two groups were separated on the basis of several species that were absent upstream of the UC unit (Appendix 2). Coefficient of variation (FCV) for annual flow, used initially to identify the flow units (Chapter 3), was correlated with dimension 2 ($r = 0.81$; $P = 0.05$) suggesting a potential response between the fish communities within inter-reservoir and unchannelized units. Although there were differences in community composition among years within units, among-unit differences were generally greater than within-unit differences. We also performed a separate MDS analysis on the four upper most hydrologic units to further identify relations among units, but the ordination was nearly identical to the analysis using all data and is not presented here.

Our ANOSIM2 test for fish community differences showed a significant hydrologic unit effect ($r = 0.92$; $P < 0.01$) which supports the ordination differences identified in Figure 2. However, we did not detect any year effects ($r = 0.20$; $P < 0.96$). Since we could demonstrate no significant year effects on the abundance and species composition of the fish community, we focused further analyses on the general morphological, functional, and life history differences among the six flow units by combining all three years of data.

We collected 106 species, exclusive of hybrids, throughout the course of the three year study (Appendix 2). The mean number of species collected in each hydrologic unit was fairly constant throughout the upper two thirds of the river, with a marked increase in the two channelized units (Figure 3). Species similarities within each unit were relatively high (>65%) over the three years of study (Table 3). However, among-unit comparisons showed varying degrees of similarity. Generally, units found in close geographic proximity had higher similarities than did units separated by larger distances. Fish communities from the upper and lower extremes had a similarity of less than 45% among the UU and LC units. Likewise, the inter-reservoir units were typically most dissimilar compared to all other units (Table 3). The percent composition of large river species was typically over 80% of the standardized total catch throughout the Missouri and lower Yellowstone Rivers (Figure 3). Percent composition of Pflieger's (1989) large river species was lowest in the inter-reservoir units, especially the IR-I unit, where the composition of large river species was 20%.

Nearly all of the continuous morphological and life-history characteristics differed significantly among units (Table 4). Fish communities from the upper river had significantly higher mean shape factors indicating a more elongate body shape. This was predominantly due to the high abundances of taxa like flathead chubs and Hybognathus spp. in the unchannelized and IR-II units and longnose suckers Catostomus catostomus in the IR-I unit. Swim factor was lowest in the channelized portion of the Missouri River suggesting a large component of individuals capable of prolonged swimming. In these units gizzard shad Dorosoma cepedianum were most abundant and had one of the lowest swim factor scores. Age at maturity and length at maturity were both highest in the IR-I unit due to high longnose sucker abundances that had much higher scores for both characteristics than most of the other highly abundant species caught in other units (Appendix 2). Mean clutch size was highest in the IR-II, UC, and LC units due to the proportion of river carpsuckers Carpiodes carpio, common carp Cyprinus carpio and gizzard shad that all have high mean clutch sizes. Maximum length showed no clear among-unit trends and average life span did not differ significantly throughout the river system.

Among-unit comparisons of the categorical functional and life-history characteristics were also significantly different (Table 5). Tolerances to silt and turbidity were generally high in all units, but mean of tolerance to silt generally decreased downstream; whereas tolerance to turbidity showed the opposite longitudinal trend, being lowest in the unchannelized units of the Missouri and lower Yellowstone Rivers.

We found marked differences in the proportional composition of the trophic guilds among flow units (Figure 4a). The upper unchannelized units were dominated by herbivorous (e.g., Hybognathus spp.) and invertivorous species (e.g., flathead chubs, sturgeon chubs Macrhybopsis gelida) (Table 5; Figure 4a). Moving downstream, there were several abrupt changes in relative abundance of trophic guilds among flow units. Proportional trophic guild composition changed dramatically between the UU and IR-I units, which are separated spatially by Ft. Peck Reservoir. Herbivores and general invertivores declined precipitously in this transition, whereas omnivores and benthic invertivores increased greatly in proportion. The IR-II unit, located between isolated sections of the IR-I unit, differed from the IR-I unit in having a much larger proportion of general invertivores and a much lower proportion of benthic invertivores. The channelized units showed a dramatic increase in the proportion of planktivores, predominantly gizzard shad.

There were also differences in the proportional composition of current preferences among flow units (Table 5; Figure 4b). The upper unchannelized units were dominated by species with either fast or moderate water velocity preferences. The transition from the UU to IR-I unit was characterized by a precipitous decline in fast and moderate velocity preferences, and a large increase in slow velocity preference. Velocity preferences were fairly even in the IR-II unit with no category accounting for more than 34% of the community. The channelized units had proportional preferences similar to the IR-I unit, with species preferring slow velocity dominating. However, moderate preference was much more prevalent in the channelized unit, accounting for over 30% of the community in both UC and LC units. Species preferring fast current included shovelnose sturgeon Scaphirhinchus platorynchus, blue sucker Cycleptus elongatus, sicklefin chub M. meeki and sturgeon chub. The moderate flow preference group was made up largely of walleye Stizostedion vitreum, sauger S. canadense, and several small cyprinid species like emerald shiner. Deeper bodied species like bigmouth buffalo Ictiobus cyprinellus, freshwater drum, and river carpsuckers made up a large proportion of the slow current preference group throughout the river. Common carp, gizzard shad, and goldeye Hiodon alosoides were fairly prevalent generalist species (Appendix 2).

The proportional composition of substrate preferences were also different among flow units (Table 5). Preference for sand dominated upstream from the reservoirs, and in the IR-II unit. Preference for gravel was greater than 40% in the IR-I unit, but well below 20% in all other units. The channelized units were similar with low percentages of gravel and sand preference, and general and pelagic preferences of roughly 40% each. Species preferring gravel substrate included blue suckers and shorthead redhorses Maxostoma macrolepidotum; whereas, the most abundant species preferring sand included emerald shiners, Hybognathus spp., and many of the other small bodied cyprinids. Substrate generalist species consisted of common carp, channel catfish, and river carpsuckers. The pelagic preference was almost exclusively gizzard shad in the channelized units.

The proportional composition of spawning substrate preference also differed significantly among units, shifting from dominance of gravel, sand, and structure in the unchannelized units, to dominance of gravel spawners in the inter-reservoir units, to a high percentage of general and pelagic spawners in the channelized units (Table 5; Figure 5b). The inter-reservoir units had a high proportion of gravel spawners as well. Species preferring gravel spawning substrate included longnose suckers, white suckers Catastomus commersoni, and shovelnose sturgeon. The most abundant species preferring sand included members of the genus Notropis, and river carpsuckers. There was also an increase in the preference of underwater structure during spawning in the inter-reservoir and channelized units. The most abundant species preferring this substrate were common carp and channel catfish. We also observed an increase in the proportion of pelagic spawners which consisted mainly of gizzard shad and freshwater drum.

Correlation analysis of morphological, functional, and life history characteristics with the individual flow variables used to define flow units revealed few significant relations, suggesting that the among-unit differences cannot be explained in terms of any single defining flow variable. However, along a gradient of increasing hydrologic alteration (from Galat and Lipkin 2000) that takes several flow variables into account, there were significant decreases in shape factor ($r = -0.88$; $P < 0.05$), age at maturity ($r = -0.96$; $P = 0.01$), and proportion of fast velocity species ($r = -0.91$; $P = 0.03$) and an increase in the proportion of slow velocity species ($r = 0.92$; $P = 0.03$) for all reaches of the river, with the exception of the IR-II unit that was not included in their analysis.

Discussion

Fish community structure in lotic communities have been evaluated by morphology (Gatz 1979), functional groups (Grossman et al. 1982; Poff and Allan 1995) and life-history characteristics (Mahon 1984) and our analyses provide a similar framework to assesses community structure within the Missouri River basin. However, it is not without complications. Ideally, relating structure to one or two variables is preferred due to the ease of interpretation and there is some evidence that flow can be used in such a manner. Toner and Keddy (1997) found that only two flow variables were needed to identify riparian wetland vegetation types along regulated rivers. Our results suggest a more complex, multivariate relation between flow and community structure, but we were able to detect differences in fish community structure.

Our results show that there are differences in fish community structure and abundance patterns among the six flow units. The strongest pattern in our data suggests that the largest differences lie between the channelized and the upstream units. Within these two groups, species abundance structures also appear different (Figure 2). A possible explanation for differences among these communities is the effect of dams blocking migration. In unregulated rivers, we would expect a gradual increase in species richness moving downstream (Vannote et al. 1980), but when dams are placed on these rivers the physical barriers can impede upstream movements, effectively isolating above dam communities from their downstream species source pools.

In addition to being barriers to movement, dams change many water quality and habitat characteristics as well (Ward and Stanford 1983). Water quality parameters such as turbidity and temperature are often changed as water passes through impoundments due to the settling sediments and location of the water release in relation to thermal stratification of the reservoir. The loss of sediment in released water changes substrate and channel dynamics, frequently resulting in a degrading channel (Hammad 1972). Increased light penetration and exposure of coarse substrates may result in increased autotrophy, with a variety of potential consequences for higher trophic levels (Voelz and Ward 1991). This process essentially resets many biotic and abiotic characteristics, often making the conditions immediately downstream from dams similar to headwater areas. Fish and other aquatic organisms adapted to conditions prior to alteration are then regionally extirpated because they are not well suited to their newly created environment. The result is a loss in species richness and this effect could help explain the large differences in richness observed between the inter-reservoir and channelized units.

The above ideas give an explanation for general differences in species richness along the Missouri and lower Yellowstone Rivers, but they do not provide detailed insight into defining the community structure. Certainly there are many influences on lotic fish community structure (Schoener 1987), but flow appears to be an important abiotic factor in these systems (Poff and Allan 1995). Additionally, flow probably reflects differences in other factors including thermal regime (Coon 1987) and habitat stability and availability (Bain et al. 1988) thereby providing a reasonable gauge to define fish community structure.

Poff and Allan (1995) documented community structure patterns in several small streams that were consistent with theoretical predictions of more trophic generalists and tolerant species in hydrologically variable environments (sensu Poff and Ward 1989). Here, we examined one continuous system where the overall differences in flow characteristics can be subtle, making it difficult to identify one unit as more variable than another. However, we can still use these units as a foundation for comparisons among fish communities.

An alternative to evaluating riverine fish communities solely on flow variability may be assessment of the degree of alteration to the flow regime as an aggregate descriptor of flow and environmental variability. Zampella and Bunnell (1998) found that fish assemblage changes were associated with gradients of watershed disturbance in New Jersey Pineland streams. On the Missouri and lower Yellowstone Rivers, Galat and Lipkin (2000) reported that the degree of alteration was moderate for flows in the unchannelized reaches, high in the inter-reservoir and upper portion of the UC unit, then declined to a more moderate level proceeding downstream. Flows through the inter-reservoir units are much different than prior to alteration and typically have very little variation on an annual scale compared to the natural hydrograph that typically has periods of high flow in the spring and lower flows in late fall and winter (Chapter 2; Hesse and Mestl 1993). So, by using degree of alteration as a measure of change in flow regimes for each unit, as a replacement to flow variability, we might predict that the inter-reservoir and UC units would consist of more generalists and species not well adapted to the pre-alteration conditions due to their higher degree of alteration (sensu Poff and Ward 1989). Our results provide some support for this hypothesis because we did find significant decreases in proportion of fast velocity preference and shape factor values, coupled with an increase in proportion of slow velocity preference species with increased flow alteration. This suggests that species from units with higher degrees of alteration tend to be deeper bodied and not well suited for more natural flow regimes that still exist to some extent in the extreme units. This also suggests a shift away from the large river life-history traits such as a large proportion of high velocity preference and high shape factor values found in the nearby unchannelized units. Additionally, the lower percentage of large river species in the inter-reservoir units, especially in the IR-I unit, suggest fish communities that are not similar to riverine communities found elsewhere in this system, further supporting our hypothesis.

We can also use this gradient of alteration to identify differences among other flow units. For example, the unchannelized units differ from the other units because they have a large component of herbivores and fast velocity preference individuals that are not present elsewhere (Figure 4). While these differences are probably due to many factors including longitudinal gradients of functional group and species zonation, we can nonetheless identify these unique communities based on their flow characteristics.

Fish communities from the channelized units are also quite different beyond the aforementioned richness and abundance differences. Gizzard shad were the most abundant species which strongly contributed to the differences in swim factor (Table 4). Swim factor was significantly lower in these two units implying an ability for sustained swimming which is characteristic of many pelagic species (Wooton 1990).

The inter-reservoir units are most strongly influenced by flow alteration along the Missouri River (Galat and Lipkin 2000; Chapter 2) and changes in morphological, functional, and life-history characteristics were most pronounced through this portion of the river. For example, there were no major changes in proportions of any functional characteristic between the two unchannelized units and between the two channelized units (Figure 4 and 5). Most of the major changes occurred in transition into and out of the inter-reservoir units located in the highly impounded middle portion of the river. An artifact of reservoir influences is the introduction or increased abundance of more lacustrine fish populations. The impact of these lacustrine fish species on riverine fish communities is not currently known. Many of the species found in this part of the river were deeper bodied individuals like freshwater drum and river carpsuckers or slow water velocity preference species like yellow perch Perca flavescens, which makes them less adapted to maintaining their position in swift currents associated with spring flows in the upper and lower units.

Patterns in tolerance to silt and turbidity are two interesting variables because they have a very different meaning on the Missouri River compared to the small streams where these metrics were first developed. In small streams, silt and turbidity are generally associated with stream degradation (Karr et al. 1986), but prior to alteration the Missouri River was extremely turbid and silt laden (Funk and Robinson 1974). Presumably, most of the endemic fish species in the Missouri River system would be adapted to and tolerant of silt and turbidity. Our data support this presumption with both metrics indicating that fish communities from all units had fairly high tolerances, but tolerance to silt showed a slight decline moving downstream; whereas, tolerance to turbidity increased moving downstream (Table 5). In the context of the Missouri River system then, these two metrics are probably not as valuable in describing differences among communities as they may be in smaller streams or less turbid large rivers.

We have generally discussed differences in fish community structure among the unchannelized, inter-reservoir, and channelized zones rather than specific units to this point.

The main reason for this is that these differences reflect the large-scale alterations found throughout the Missouri River system and community differences were readily identified. There were, however, distinct differences among some units within these larger scaled zones. The IR-I and IR-II units exhibited large differences in several of the measures we present, especially the differences in proportion of general and benthic invertivores and velocity preference (Figures 4). However, differences between the UU and UYS units and the UC and LC units were less obvious with no large shifts in proportion of functional groups for either set of flow units. Our ordination did show some separation between the UC and LC units, but the unchannelized units were nearly identical (Figure 2).

Pegg and Pierce (Chapter 3) concluded that flow regimes in the uppermost and lowermost portions of the river exhibit some similarities. Galat and Lipkin (2000) reported similar results showing that amount of hydrological alteration was lowest in these portions of the river as well. Since we were attempting to identify fish community relationships with flow regime, we might have expected some community similarities among upper and lower portions of the river, mirroring the flow results. We found, on the contrary, a low similarity (Table 3) and quite different functional and life-history patterns (Tables 4 and 5) between the upper and lowermost units so this hypothesis was not clearly supported. It appears that the community patterns we found reflect a combination of effects: natural river zonation patterns, blockage of migration due to dams, as well as a variety of changes in flow regime and other environmental effects of human alteration.

Large river systems are by nature in limited supply, and unfortunately there remain even fewer unaltered large river systems (Benke 1990) to use as controls for evaluating the effects of human alteration. The imperative to rigorously evaluate these effects remains, however, and novel approaches (e.g., Simon and Emery 1995) will be required to overcome the limitations inherent in conventional statistical approaches. Comparison of communities from sites *within* a single river system, as we have done here, will be the only practical approach in many situations. By quantifying how flow conditions currently differ among portions of the river, as we have done previously (Chapter 3), relating flow conditions to alteration in some portions of the river (Galat and Lipkin 2000: Chapter 2), and demonstrating community differences among these areas, as we have done here, we believe we have demonstrated not only relationships of the fish community with flow characteristics, but some likely consequences of human alteration of the Missouri River system.

The clearest pattern in our results was the distinction of communities in the channelized portion of the river below the mainstem reservoirs from all parts of the Missouri and lower Yellowstone Rivers. This distinction was due in large part to the higher species richness found in the channelized portion of the river. Our data also suggest the morphological, functional, and life-history structures in the inter-reservoir units consist of more generalist species which supports our prediction of increasing generalists with an increase in the degree of alteration for each flow unit.

Few studies have assessed the functional organization of fish communities in a large river system as we have done here. Our data provide some evidence that fish communities are linked to flow regimes, but that other, and possibly greater influences including the longitudinal zonation of species, effects of dams blocking migration, and other human alterations are important as well. While there is a continuing concern to identify community patterns as they relate to environmental conditions (Matthews and Heins 1987), identifying these patterns in a large river system will be a major challenge for stream ecologists.

APPENDIX 1. MORPHOLOGICAL, FUNCTIONAL, AND LIFE-HISTORY CHARACTERISTICS FOR FISH SPECIES CAUGHT ALONG THE MISSOURI AND LOWER YELLOWSTONE RIVERS

Table 1. List of 106 fish species collected from the Missouri and lower Yellowstone rivers 1996-1998. Included are the adjusted total catch by each flow unit, life-history, functional, and morphological characteristics, and large river (LRS) classifications for each species. See text and Table 2 for variable description and names.

	Flow Units																					
SPECIES	UYS	UU	IR-I	IR-II	UC	LC	AM	LM	ML	LS	MC	PC	WC	GLD	CUR	SUB	SPS	SLT	TRB	SWM	SHP	LRS
Gizzard Shad, *Dorosoma cepdianum*	0.0	0.0	0.0	0.0	5743.9	4732.4	2	251	486	14	281044	0	3	6	3	8	8	1	2	0.3	3.4	X
Flathead Chub, *Platygobio gracilis*	5310.3	2808.2	92.4	856.8	3.3	2.7	1	85	324	10	4974		2	3	1	3			1	0.5	4.9	X
Emerald Shiner, *Notropis atherinoides*	602.3	2034.4	56.6	31.0	2573.5	2127.1	1		103	3		0	3	3	2	5	3	1	1	0.4	6.1	X
River Carpsucker, *Carpiodes carpio*	1126.8	97.8	199.1	235.7	766.7	858.3	3	240	594	11	102766	0	2	2	3	5	3	1	1	0.4	3.6	X
Western Silvery Minnow, *Hybognathus argyritis*	1259.9	1490.2	23.8	22.5	1.4	1.0		75	110	4			1	1	3	4	4	1	1			X
Longnose Sucker, *Catastomus catastomus*	11.0	88.0	2370.9	13.6	0.0	0.0	5	369	462	12	17000	1	2	4	3		2			0.6	7.1	
Plains Minnow, *Hybognathus placitus*	1385.8	993.5	9.3	13.7	2.3	6.2	1	48	125	3	817	0	1	1	2	3		2	1	0.4	4.7	X
Goldeye, *Hiodon alosoides*	624.8	244.5	284.5	716.3	188.6	86.5								3	4	3	2	1	1	0.4	4.2	X
Channel Catfish, *Ictalurus punctatus*	592.7	130.0	46.5	77.6	494.1	653.0	4	358	976	14	7977	3	1	2	2	5	7	1	1	0.6	6.7	X
Sturgeon Chub, *Macrhybopsis gelida*	1223.1	290.8	14.0	125.0	6.7	10.0	2	43	100	4	5310		1	3	1	3		3	1	0.5	6.7	X
Common Carp, *Cyprinus carpio*	194.1	150.3	122.8	294.7	282.8	292.8	2	279	1080	20	1122000	0	1	2	4	5	7	1	1	0.5	3.6	X
White Sucker, *Catastomus commersoni*	39.8	61.5	858.7	225.2	0.8	0.0	6	260	589	10	60325	1	2	2	3	2	2	1	2	0.5	4.9	
Shovelnose Sturgeon, *Scaphirhynchus platorynchus*	450.5	106.7	115.8	86.7	106.7	126.8	7	635	853	35	25000	0	1	4	1	3	2	2	1	0.2	11.6	X
Freshwater Drum, *Aplodinotus grunniens*	22.0	125.1	4.8	14.7	421.2	354.2	4	342	543	17	275000	0	2	4	3	4	8	1	1	0.5	3.5	X
Red Shiner, *Cyprinella lutrensis*	0.0	0.0	4.4	0.0	180.6	656.5	1	30	90	3	750	2	3	3	4	5	2	1	1	0.5	3.7	X
Shorthead Redhorse, *Moxostoma macrolepidotum*	87.0	296.7	30.3	122.5	69.6	9.3	3	330	660	9	20325	1	2	4	2	2	2	3	1	0.5	4.8	
Quillback, *Carpiodes cyprinus*	0.0	0.0	0.0	0.0	470.8	7.6	2	156	660	10	39507	0	1	2	3	2	2	1	2	0.5	3.7	
Fathead Minnow, *Pimphales promelas*	90.5	0.5	257.7	64.1	8.9	1.5	1	48	74	2	355	3	3	2	3	5	7	1	1	0.5	5.3	
Sicklefin Chub, *Macrhybopsis meeki*	124.0	133.5	0.0	81.0	4.0	47.3	2	43	109	4			1		1	3		3	1	0.5	6.4	X
Flathead Catfish, *Pylodictus olivaris*	0.0	0.0	0.0	0.0	183.2	168.1	5	485	1410	19	9100	3	1	5	2	5	7	1	1	0.8	8.1	X
Longnose Dace, *Rhynichthys cataractae*	213.5	102.6	5.0	12.6	0.0	0.0	2	74	119	5	560	1	2	4	1	2	2	2	2	0.5	6.3	
Sauger, *Stizostedion canadense*	84.0	83.1	18.3	52.6	55.6	21.0	5	318	490	12	52500	1	2	5	2	5	2	1	1	0.4	6.7	X
River Shiner, *Notropis blennius*	0.0	0.0	0.0	0.0	243.5	63.8	3	51	132	5	2500		2	3	2	3	3	2	1	0.5	5.0	X
Spotfin Shiner, *Cyprinella spiloptera*	0.0	0.0	0.0	0.0	292.6	0.4	1	47	106	4	56	1	3	3	1	2	7	1	1	0.4	5.4	
Bluegill, *Lepomis macrochirus*	0.0	0.0	0.8	0.0	58.6	224.1	2	102	384	9	19225	3	2	3	3	5	5	2	2	0.5	2.6	
Spottail Shiner, *Notropis hudsonius*	32.8	118.4	69.0	58.5	4.0	0.0	2	66	117	3	1614	0	3	3	3	2	3	2	2	0.5	4.8	X
Walleye, *Stizostedion vitreum*	56.4	36.1	42.8	77.1	67.1	2.7	5	394	790	14	82700	1	2	5	2	5	7	2	2	0.5	5.6	

Table 1. (continued)

SPECIES	Flow Units: UYS	UU	IR-I	IR-II	UC	LC	AM	LM	ML	LS	MC	PC	WC	GLD	CUR	SUB	SPS	SLT	TRB	SWM	SHP	LRS
Stonecat, *Noturus flavus*	140.7	51.2	2.5	28.0	2.9	5.7	2	64	267	9	205	3	1	4	2	1	7	3	3	0.8	7.7	
Sand Shiner, *Notropis stramineus*	0.0	0.0	0.8	0.0	155.7	68.6	1	36	64	3	350	1	3	3	2	3	2	3	2	0.5	6.6	
Shortnose Gar, *Lepisosteus platostomus*	1.0	0.0	0.0	1.0	77.0	125.6	3	330	800	20	36000	1	3	5	3	4	6	1	1	0.5	11.4	X
White Crappie, *Pomoxis annularis*	49.7	48.6	1.5	56.0	29.3	15.3	2	150	505	8	39922	3	3	5	3	5	2	1	1	0.4	3.5	
White Bass, *Morone chrysops*	6.8	0.0	0.8	3.6	99.4	85.0	2	254	381	9	527850	1	3	5	2	2	2	2	2	0.5	3.5	X
Smallmouth Buffalo, *Ictiobus bubalus*	20.2	18.3	21.6	44.1	39.4	40.4	4	374	909	19	233031	0	2	2	3	5	5	2	2	0.5	3.5	
Northern Pike, *Esox lucius*	48.0	27.1	38.3	54.0	5.9	0.3	3	401	1296	24	32000	1	3	5	3	6	6	3	3	0.5	7.7	
Bigmouth Buffalo, *Ictiobus cuprinellus*	3.9	1.7	20.9	103.0	18.5	4.8	4	406	967	12	400000	0	2	2	3	5	5	1	1	0.4	3.4	X
Blue Catfish, *Ictalurus furcatus*	0.0	0.0	0.0	0.0	20.5	99.5	5	681	1550	21		2	1	2	2	2	7	3		0.4	4.4	X
Silver Chub, *Macrhybopsis storeriana*	0.0	0.0	0.0	0.0	67.0	50.0								4	2	4	8	1	2	0.4	5.4	X
Yellow Perch, *Perca flavescens*	0.0	24.3	21.4	22.0	41.7	0.0																
Speckled Chub, *Macrhybopsis aestivalis*	0.0	0.0	0.0	0.0	12.5	87.5								4	1	3	B	3	2	0.3	5.7	X
Burbot, *Lota lota*	17.0	69.0	4.5	6.0	0.3	0.0	3	419	838	16	628808	0	2	5	3	5	2	2	2	0.6	8.2	X
Black Crappie, *Pomoxis nigromaculatus*	0.0	76.2	1.6	0.0	8.0	4.3	2	140	472	9	37795	3	3	5	3	5	2	2	2	0.4	3.1	
Blue Sucker, *Cycleptus elongatus*	17.5	8.2	9.6	10.0	29.6	8.6	6	610	1030	13	117889	0	1	4	1	2	1	3	1	0.4	4.6	X
Green Sunfish, *Lepomis cyanellus*	7.0	0.0	0.0	0.0	34.5	39.2	1	66	259	6	32000	3	2	3	4	5	5	1	1	0.5	3.2	
Smallmouth Bass, *Micrpterus dolomieu*	1.0	1.2	14.8	2.0	55.6	0.0	3	292	686	14	7708	4	2	5	2	2	2	3	3	0.6	4.5	
Mosquitofish, *Gambusia affinis*	0.0	0.0	0.0	0.0	1.2	70.8	0	30	59	1	40	4	3	6	3	6	8	1	1	0.6	4.4	
Largemouth Bass, *Micropterus salmoides*	0.0	0.0	0.0	0.0	34.5	29.8	2	250	701	15	25544	4	2	5	3	2	1	2	2	0.4	3.9	
Longnose Gar, *Lepisosteus osseus*	0.0	0.0	0.0	0.0	20.3	33.1	6	500	1370	30	27830	1	3	5	3	8	6	2	2	0.5	12.7	
Golden Shiner, *Notemigonis crysoleucas*	0.0	0.0	0.8	0.0	44.4	1.9	2	64	259	9	101000	1	3	2	3	4	6	1	2	0.4	4.3	
Orangespotted Sunfish, *Lepomis humilis*	0.0	0.0	0.0	0.0	28.6	16.0	1	61	137	4	1385	3	2	3	4	5	5	1	1	0.5	2.9	
Creek Chub, *Semotilus atromaculatus*	27.6	0.0	3.0	12.6	0.8	0.0	3	76	320	8	3886	3	3	2	3	2	2	1	1	0.5	5.1	
Bigmouth Shiner, *Notrpois dorsalis*	0.0	0.0	0.0	0.0	35.2	6.6								4	2	3	3	2	1	0.5	5.6	
Brassy Minnow, *Hybognathus hankinsoni*	0.0	0.0	0.0	0.0	37.3	0.0	2	56	75	4	1750		1	2	3	3	6	2	2	0.5	5.2	
Spotted Bass, *Micropterus punctulatus*	0.0	0.0	0.0	0.0	0.0	32.1	3	216	505	8	11911	3	2	5	2	2	2		2	0.4	3.8	
Mimic Shiner, *Notropis volucellus*	0.0	0.0	0.0	0.0	2.0	28.1	1	38	65	3	367		3	6	2	1	1	2	2	0.4	6.3	X
Johnny Darter, *Etheostoma tetrazonum*	0.0	0.0	8.2	0.0	6.8	0.3	1	43	73	5	115	3	1	3	3	3	7	2	1	0.5	7.3	
Bluntnose Minnow, *Pimphales notatus*	0.0	0.0	0.0	0.0	0.5	11.7	2	51	79	3	297	3	3	4	2	5	7	1	1	0.5	5.7	

Table 1. (continued)

SPECIES	Flow Units: UYS	UU	IR-I	IR-II	UC	LC	AM	LM	ML	LS	MC	PC	WC	GLD	CUR	SUB	SPS	SLT	TRB	SWM	SHP	LRS
Golden Redhorse, *Moxostoma erythrurum*	0.0	0.0	0.0	0.0	1.3	9.3	4	290	625	7	16689	1	2	4	3	5	2	2	2	0.4	4.7	
Rainbow Trout, *Onchorhynchus mykiss*	0.0	0.5	9.7	0.0	0.0	0.0								3	1	2	2	3	3	0.6	4.3	
Rainbow Smelt, *Osmerus mordax*	0.0	0.0	9.1	0.0	0.5	0.2								3	3	3	2			0.4	6.6	X
Bighead Carp, *Hypopthalmichthys nobilis*	0.0	0.0	0.0	0.0	2.2	7.3	6	700	1000	9		0	3	6	4		8	1	1	0.5	4.9	X
Striped Bass, *Morone saxatilis*	0.0	0.0	0.0	0.0	0.0	9.2								5	4	5	2	2	1	0.5	4.4	
Brook Silverside, Labidesthes sicculus	0.0	0.0	0.0	0.0	2.5	5.2								6	3	2	2	2	3	0.4	8.5	
Mottled Sculpin, *Cottus bairdi*	0.0	7.3	0.0	0.0	0.0	0.0								3	4	5	7	2	3	0.5	5.3	
Cisco, *Coregonus artedi*	0.0	0.5	6.8	0.0	0.0	0.0	3	246	421	10	4616	0	3	6		5	5			0.3	4.4	
Grass Carp, *Ctenopharyngodon idella*	0.0	0.0	0.0	0.0	2.9	1.9	4	872	1250	10		0	2	1	4	5	8	1	1	0.5	4.0	X
Paddlefish, *Polydon spathula*	0.0	0.0	0.0	1.0	1.0	2.7	10	1067	2235	30	139389	1	3	6	3	8	2	1	1	0.3	5.6	
Skipjack Herring, *Alosa chrysochloris*	0.0	0.0	0.0	0.0	0.0	4.2								5	1	2		3	2	0.4	44.4	X
Bullhead Minnow, *Pimphales promelas*	0.0	0.0	0.0	0.0	1.5	2.2								2	3	3	7	1	1	0.6	4.7	
Lake Whitefish, *Coregonus clupeaformis*	0.0	0.0	0.0	3.0	0.0	0.0	2	310	749	28	67892	0	2	4		5	2			0.3	5.2	
Freckled Madtom, *Noturus nocturnus*	0.0	0.0	0.0	0.0	0.0	2.9	2	51	109	4	33	3	1	4	2	3	7	1	2	0.7	6.0	
Suckermouth Minnow, *Phenacobis mirabilis*	0.0	0.0	0.0	0.0	0.0	2.8								4	2	3	2	3	1	0.4	6.2	
Black Bullhead, *Ameiurus melas*	2.0	0.0	0.3	0.0	0.5	0.0	3	254	345	9	3069	4	1	2	3	5	7	1	1	0.5	3.9	
Yellow Bass, *Morone mississippiensis*	0.0	0.0	0.0	0.0	0.0	2.5								3	3	5	2	2	2	0.4	3.6	X
Rock Bass, *Ambloplites rupestris*	0.0	0.0	0.0	0.0	2.4	0.0	3	159	279	13	4981	3	2	5	2	2	3	3	3	0.5	3.1	
Pallid Sturgeon, *Scaphirhynchus albus*	2.0	0.0	0.0	0.0	0.2	0.0	15	535	1520	41	87083		1	4	1	5		2	1	0.2	8.6	X
Goldfish, *Carrasius auratus*	0.0	0.0	0.0	0.0	1.1	1.0								2	3	5	7	1	1	0.5	3.2	
Banded Killifish, *Fundulus diaphanus*	0.0	0.0	2.0	0.0	0.0	0.0		50	76		50	1	3	6	3	3	6	2	2	0.7	6.0	
Highfin Carpsucker, *Carpiodes velifer*	0.0	0.0	0.0	0.0	0.9	1.0								1	2	2	2	3	2	0.5	3.9	
Lake Sturgeon, *Acipenser fulvescens*	0.0	0.0	0.0	0.0	0.0	1.7	20	889	2159	80	385079	1	1	4	2	5	2	3		0.3	8.5	X
Bigeye Shiner, *Notropis boops*	0.0	0.0	0.0	0.0	0.5	1.1								3	2	2		2	2	0.4	6.4	
Logperch, *Percina caprodes*	0.0	0.0	0.0	0.0	0.0	1.5	2	72	196	4	369	1	1	4	3	2	2	2	3	0.6	6.2	
Brook Stickleback, *Culaea inconstans*	0.0	0.0	0.5	1.0	0.0	0.0								3	4	5	6	1	1	0.5	5.3	
Yellow Bullhead, *Ameiurus natalis*	0.0	0.0	0.0	0.0	1.5	0.0	3	230	330	7	2961	4	1	2	3	5	7	1	2	0.8	5.6	
Chestnut Lamprey, *Ichthyomyzon castaneus*	0.0	0.0	0.0	0.0	0.0	1.2									2	5	5	1	3	0.6	9.1	X
Pearl Dace, *Margariscus margarita*	1.0	0.0	0.0	0.0	0.0	0.0								3	2	5	1	2	3	0.6	5.5	

Table 1. (continued)

SPECIES	Flow Units						AM	LM	ML	LS	MC	PC	WC	GLD	CUR	SUB	SPS	SLT	TRB	SWM	SHP	LRS
	UYS	UU	IR-I	IR-II	UC	LC																
Black Buffalo, *Ictiobus niger*	0.0	0.0	0.0	0.0	0.0	0.9								2	2	5	5	1	1	0.5	3.9	
White Perch, *Morone americana*	0.0	0.0	0.0	0.0	0.8	0.0								5	4	5	2	1	1			
Bowfin, *Amia calva*	0.0	0.0	0.0	0.0	0.0	0.7	5	610	787	24	43253	4	3	5	3	5	6	1	2	0.8	5.8	
Common Shiner, *Luxilus cornutus*	0.0	0.0	0.0	0.0	0.0	0.7								2	2	5	2	3	2	0.6	4.2	
River Redhorse, *Moxostoma carinatum*	0.0	0.0	0.0	0.0	0.6	0.0	3	264	736	12	14582	1	1	4	2	2	2	3	3	0.3	4.4	
Silverband Shiner, *Notropis exilis*	0.0	0.0	0.0	0.0	0.3	0.3									2	3		1		0.4	5.5	X
Largescale Stoneroller, *Campostoma oligolepis*	0.0	0.0	0.0	0.0	0.0	0.5								1	1	5	2	3	3	0.5	4.7	
Ghost Shiner, *Notropis buchanani*	0.0	0.0	0.0	0.0	0.3	0.3									3	3	3	2	2	0.5	5.7	
Brown Trout, *Salvelinus fontinalis*	0.0	0.5	0.0	0.0	0.0	0.0								3	2	5	2	2	2	0.4	4.8	
Chinook Salmon, *Oncorhynchus tshawytscha*	0.0	0.0	0.5	0.0	0.0	0.0								5	2	2	2	3	3	0.3	3.7	
Muskellunge, *Esox masquinongy*	0.0	0.0	0.5	0.0	0.0	0.0	4	648	1510	30	125260	0	3	5	3	6	6	3	3	0.3	6.7	
Northern Redbelly Dace, *Phoxinus eos*	0.0	0.0	0.5	0.0	0.0	0.0								6	3	5	6	1	3	0.6	5.0	
Lake Chub, Couesius plumbeus	0.0	0.5	0.0	0.0	0..0	0.0								3	3	2	2	1	1	0.4	5.2	
Spotted Gar, *Lepisosteus oculatus*	0.0	0.0	0.0	0.0	0.2	0.3								5	3	6	6	2	2	0.6	10.3	
Northern Hogsucker, *Hypentelium nigricans*	0.0	0.0	0.0	0.0	0.4	0.0								4	2	2	2	3	3	0.5	5.9	
Threadfin Shad, *Dorosoma petenense*	0.0	0.0	0.0	0.0	0.4	0.0	1	102	220	2	9550	0	3	6	2	4	7			0.4	3.6	X
Grass Pickerel, *Esox americanus vermiculatus*	0.0	0.0	0.0	0.0	0.3	0.0								5	3	6	6	3	2	0.6	7.5	
Slender Madtom, *Noturus exilis*	0.0	0.0	0.0	0.0	0.3	0.0								4	2	2	7	3	2	0.8	6.3	
Tadpole Madtom, *Noturus gyrinus*	0.0	0.0	0.0	0.0	0.3	0.0	1	55	150	3	36	3	1	4	3	5	7	2	2	0.8	4.5	
Striped Shiner, *Luxilus Chrysocephalus*	0.0	0.0	0.0	0.0	0.0	0.2								3	2	2	2	2	3	0.5	4.2	
Longear Sunfish, *Lepomis megalotis*	0.0	0.0	0.0	0.0	0.0	0.1	2	56	201	7	3361	3	2	3	2	2	2	2	2	0.6	2.5	

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Table 1. Morphological, functional, and life-history characteristics used in the analysis of fish communities in the Missouri and lower Yellowstone rivers. Variables, scoring data from Winemiller and Rose (1992), Poff and Allan (1995) and unpublished data.

Continuous Characteristics	Categorical Characteristics
Shape Factor (SHP)	Current Preference (CUR)
	1. Fast
Ratio of total length to maximum body depth	2. Moderate
	3. Slow-none
	4. General
Swim Factor (SWM)	
	Tolerance to Silt (SLT)/Turbidity (TRB)
Ratio of minimum depth of caudal peduncle to the maximum caudal fin depth	1. High
	2. Medium
	3. Low
Mean Clutch Size (MC)	
	Substrate (SUB)/Spawn Substrate (SPS)
Mean number of eggs for population at mid-point of latitudinal range	1. Cobble
	2. Gravel
	3. Sand
Length at Maturity (LM)	4. Silt
	5. General
Total length at maturation (mm)	6. Vegetation
	7. Structure (e.g., deadfalls)
Age at Maturity (AM)	8. Pelagic
Mean reported age at maturation (yr)	Water Column Preference (WC)
	1. Benthic
Longevity (LS)	2. Epibenthic
	3. Pelagic
Maximum reported age in years (yr)	
	Trophic Guild (GLD)
Maximum Length (ML)	1. Herbivore
	2. Omnivore
Reported maximum total length (mm)	3. General Invertivore
	4. Benthic Invertivore
Parental Care (PC)	5. Piscivore
	6. Planktivore
Range of parental care from 0 (no care) to 8 (intense care)	

Table 2. Correlations of adjusted species abundances with dimension scores from the MDS of fish communities in the Missouri and lower Yellowstone Rivers. Species that comprised ≥ 1% of the total catch are included with proportions listed in parentheses.

	Dimension 1		Dimension 2	
Species	*r*	*P*	*r*	*P*
Gizzard Shad (19)	-0.38	0.46	0.41	0.42
Flathead Chub (16)	0.29	0.25	0.63	0.01
Emerald Shiner (13)	-0.58	0.02	0.16	0.56
River Carpsucker (6)	-0.35	0.15	0.12	0.62
W. Silvery Minnow (5)	0.69	0.31	0.11	0.89
Longnose Sucker (4)	0.24	0.44	-0.49	0.10
Plains Minnow (4)	-0.76	0.45	0.71	0.50
Goldeye (4)	0.31	0.22	0.22	0.37
Channel Catfish (4)	-0.51	0.03	0.33	0.18
Sturgeon Chub (3)	0.24	0.34	0.51	0.03
Common Carp (2)	0.08	0.76	0.10	0.69
White Sucker (2)	0.36	0.23	-0.53	0.07
Shovelnose Sturgeon (2)	0.06	0.82	0.37	0.13
Freshwater Drum (2)	-0.71	< 0.01	-0.21	0.41
Red Shiner (2)	-0.55	0.20	0.30	0.51
Shorthead Redhorse (1)	0.27	0.29	0.32	0.21
Quillback (1)	0.56	0.33	-0.57	0.32
Fathead Minnow (1)	0.54	0.04	-0.48	0.08
Sicklefin Chub (1)	0.37	0.17	0.45	0.09
Flathead Catfish (1)	0.18	0.74	0.61	0.20
Longnose Dace (1)	-0.74	0.01	0.64	0.04
Sauger (1)	0.12	0.65	0.35	0.16
River Shiner (1)	0.51	0.30	-0.89	0.02

Table 3. Fish community similarity (%) among and within flow variability units in the Missouri and lower Yellowstone Rivers. Data analyzed were adjusted species abundances collected in 1996-1998. Within-unit similarity compares the communities among years. See text for description of flow variability units.

	UYS	UU	IR-I	IR-II	UC	LC	Within-Unit Similarity
Unchannelized Yellowstone (UYS)	100						78
Upper Unchannelized (UU)	74	100					84
Inter-Reservoir I (IR-I)	56	60	100				72
Inter-Reservoir II (IR-II)	67	69	64	100			69
Upper Channelized (UC)	46	47	43	42	100		79
Lower Channelized (LC)	43	42	34	37	71	100	76

Table 4. Mean morphological and life-history characteristics with continuous measures for each flow variability unit in the Missouri and lower Yellowstone River identified in Figure 1. Significant differences ($P < 0.05$) among units were detected for each characteristic except life span. Means sharing common superscripts are not significantly different. Numbers in parentheses are standard errors. The units are arranged longitudinally from upstream (left) to downstream (right).

	UYS	UU	IR-I	IR-II	UC	LC
Shape Factor	5.4^{ab}	5.6^{ab}	6.2^{a}	4.9^{b}	4.8^{b}	4.6^{b}
	(0.3)	(0.2)	(0.2)	(0.3)	(0.2)	(0.2)
Swim Factor	0.48^{a}	0.47^{a}	0.55^{b}	0.46^{a}	0.42^{c}	0.41^{c}
	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)	(0.01)
Mean Clutch Size	$35{,}333^{a}$	$38{,}153^{a}$	$51{,}742^{a}$	$165{,}098^{b}$	$171{,}145^{b}$	$193{,}631^{b}$
	(25,229)	(30,355)	(25,391)	(65,417)	(26,142)	(27,171)
Length at Maturity	150^{a}	140^{a}	321^{b}	209^{ac}	240^{c}	258^{bc}
	(26)	(26)	(17)	(27)	(16)	(18)
Age at Maturity	2.0^{a}	1.7^{a}	4.7^{b}	2.7^{a}	2.2^{a}	2.4^{a}
	(0.3)	(0.3)	(0.2)	(0.3)	(0.2)	(0.2)
Maximum Length	389^{ab}	307^{a}	507^{b}	546^{b}	427^{ab}	494^{b}
	(46)	(44)	(31)	(59)	(40)	(44)
Lifespan	10.3	8.4	11.8	11.8	10.0	11.8
	(1.1)	(1.2)	(0.8)	(1.2)	(0.8)	(0.9)

Table 5. Mean and median life-history characteristics with categorical measures for each flow variability unit in the Missouri and lower Yellowstone Rivers identified in Figure 1. There were significant ($P < 0.05$) unit effects for all characteristics. The top number is the mean and the bottom number is the median with the associated 25 and 75 quartiles in parentheses. The units are arranged longitudinally from upstream (left) to downstream (right).

	UYS	UU	IR-I	IR-II	UC	LC
Trophic Guild	2.6 3 (2-4)	2.4 3 (2-4)	3.2 3 (2-5)	2.9 4 (2-5)	3.6 4 (2-5)	3.6 4 (2-5)
Silt Tolerance	1.7 2 (1-2)	1.6 2 (1-3)	1.2 2 (1-3)	1.4 1 (1-2)	1.2 2 (1-2)	1.2 2 (1-2)
Turbidity Tolerance	1.1 1 (1-2)	1.0 1 (1-2)	1.5 1 (1-2)	1.2 1 (1-2)	1.4 1 (1-2)	1.5 1 (1-2)
Water Column	1.8 2 (1-3)	2.1 2 (1-3)	2.0 2 (1-3)	1.8 2 (1-3)	2.2 2 (1-3)	2.1 2 (1-3)
Parental Care	0.9 1 (0-3)	0.4 1 (0-2)	1.0 1 (0-3)	0.8 1 (0-1)	0.4 1 (0-3)	0.5 1 (0-3)
Current Preference	1.7 3 (2-3)	1.8 3 (2-3)	2.9 3 (2-3)	2.5 3 (2-3)	2.5 2 (2-3)	2.6 3 (2-3)
Substrate Preference	3.4 4 (2-5)	3.6 5 (2-5)	3.2 4 (2-5)	3.5 4 (2-5)	4.4 4 (2-5)	4.7 4 (3-5)
Spawning Substrate	3.6 3 (2-6)	3.1 2 (2-6)	2.5 3 (2-6)	3.6 3 (2-6)	3.5 5 (2-7)	3.7 3 (2-7)

List of Figures

Figure 5. Percent composition for (A) substrate preferences and (B) spawning substrate preferences by flow unit in the Missouri and lower Yellowstone Rivers (Figure 1). Percentages were calculated using all data collected over the three years of study. The units are longitudinally ordered from upstream (left) to downstream (right).

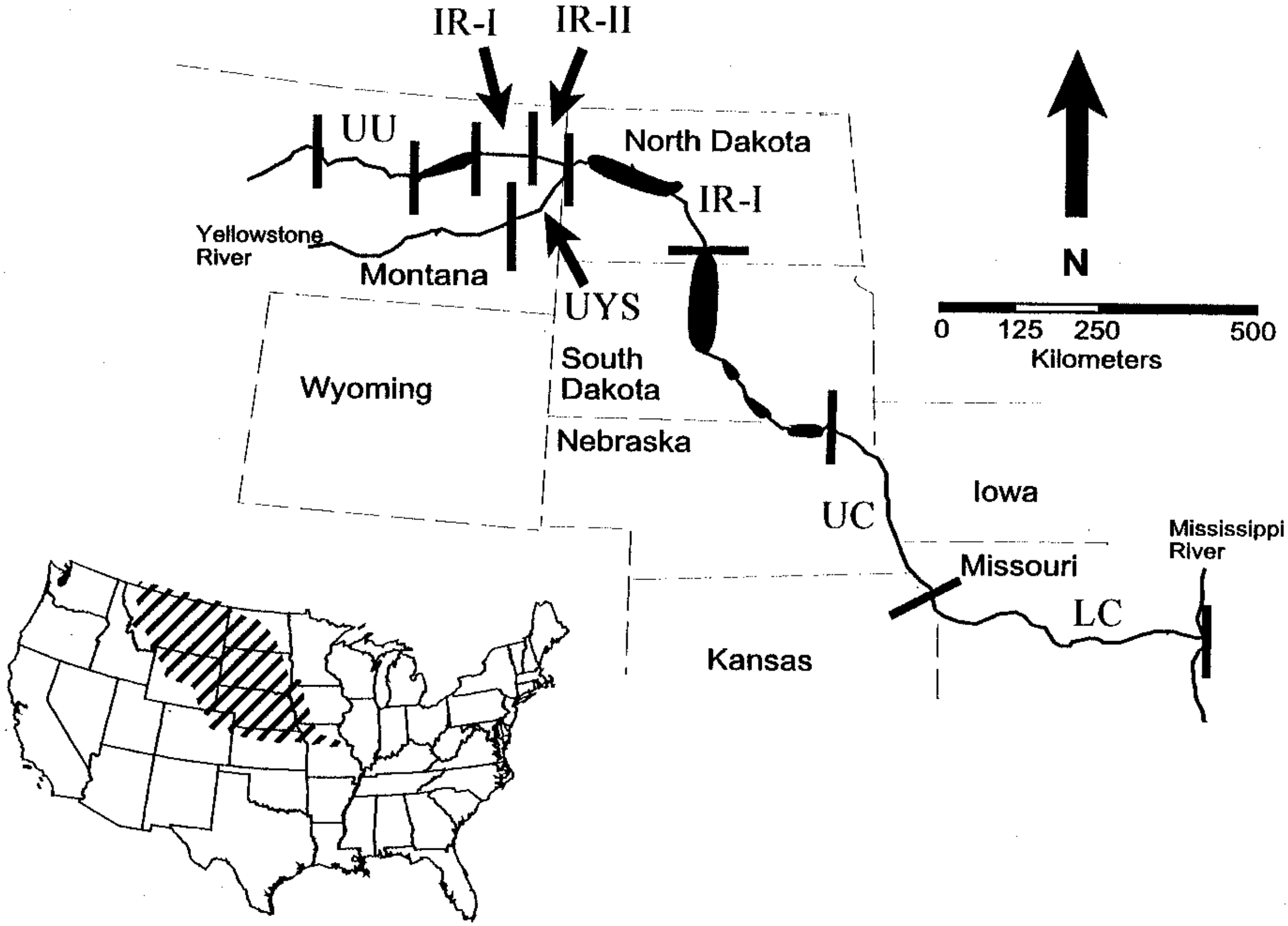
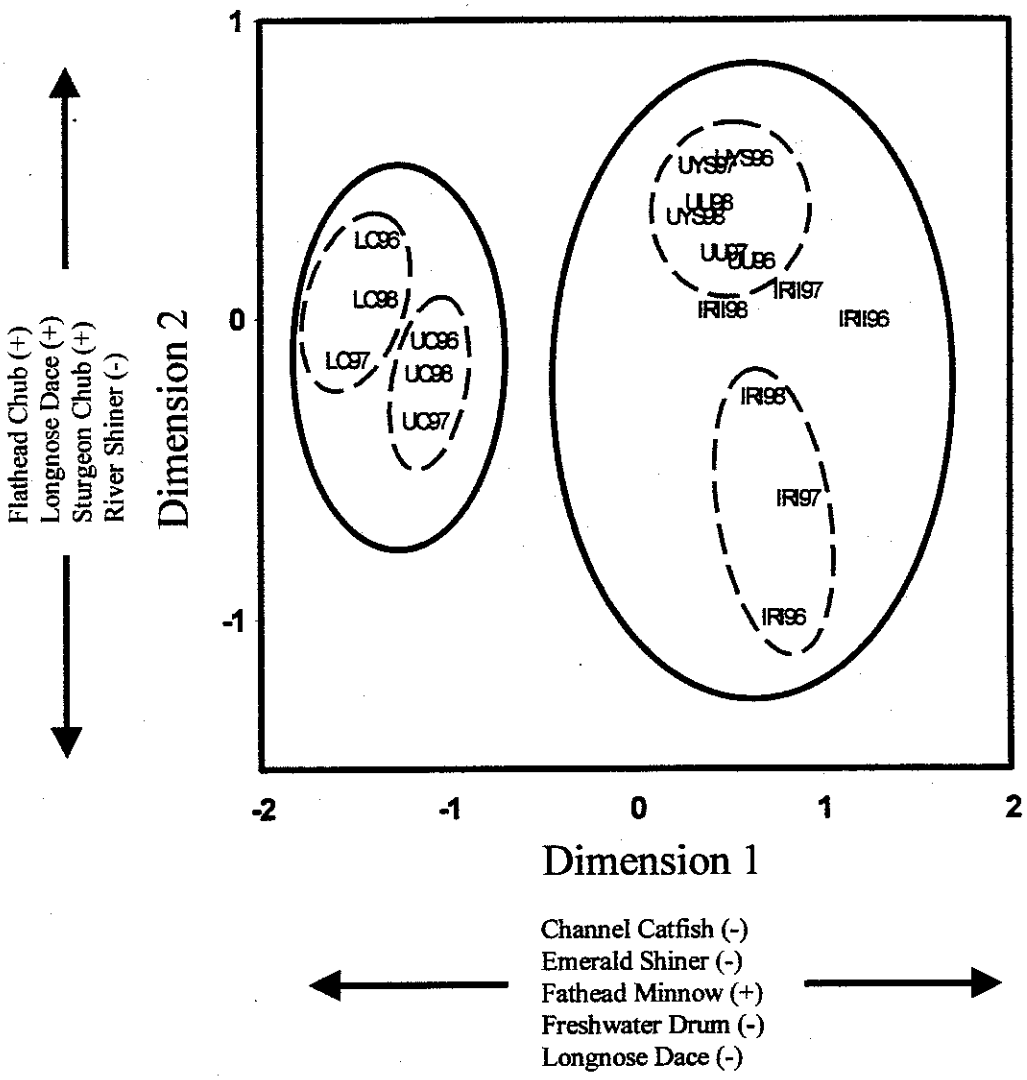

IR-I
IR-II
UU
North Dakota
IR-I
Yellowstone River
Montana
UYS
South Dakota
Wyoming
Nebraska
Iowa
UC
Missouri
Mississippi River
LC
Kansas
N
0 125 250 500
Kilometers

Figure 1.



Flathead Chub (+)
Longnose Dace (+)
Sturgeon Chub (+)
River Shiner (-)
Dimension 2
1
0
-1
LC96
LC98
LC97
UC96
UC98
UC97
IRII97
IRII98
IRII96
IRI98
IRI97
IRI96
-2
-1
0
1
2
Dimension 1
Channel Catfish (-)
Emerald Shiner (-)
Fathead Minnow (+)
Freshwater Drum (-)
Longnose Dace (-)

Figure 2.

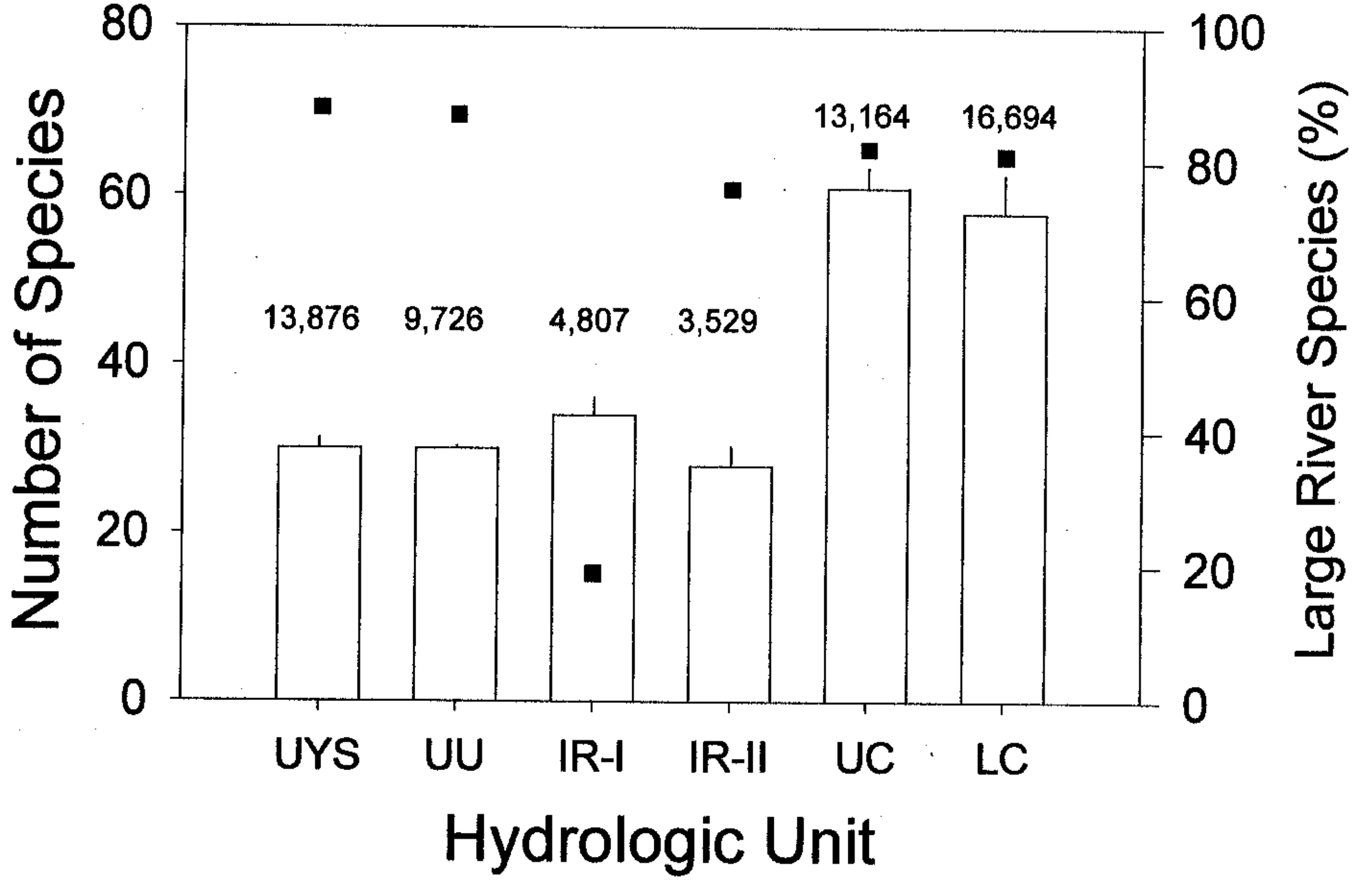
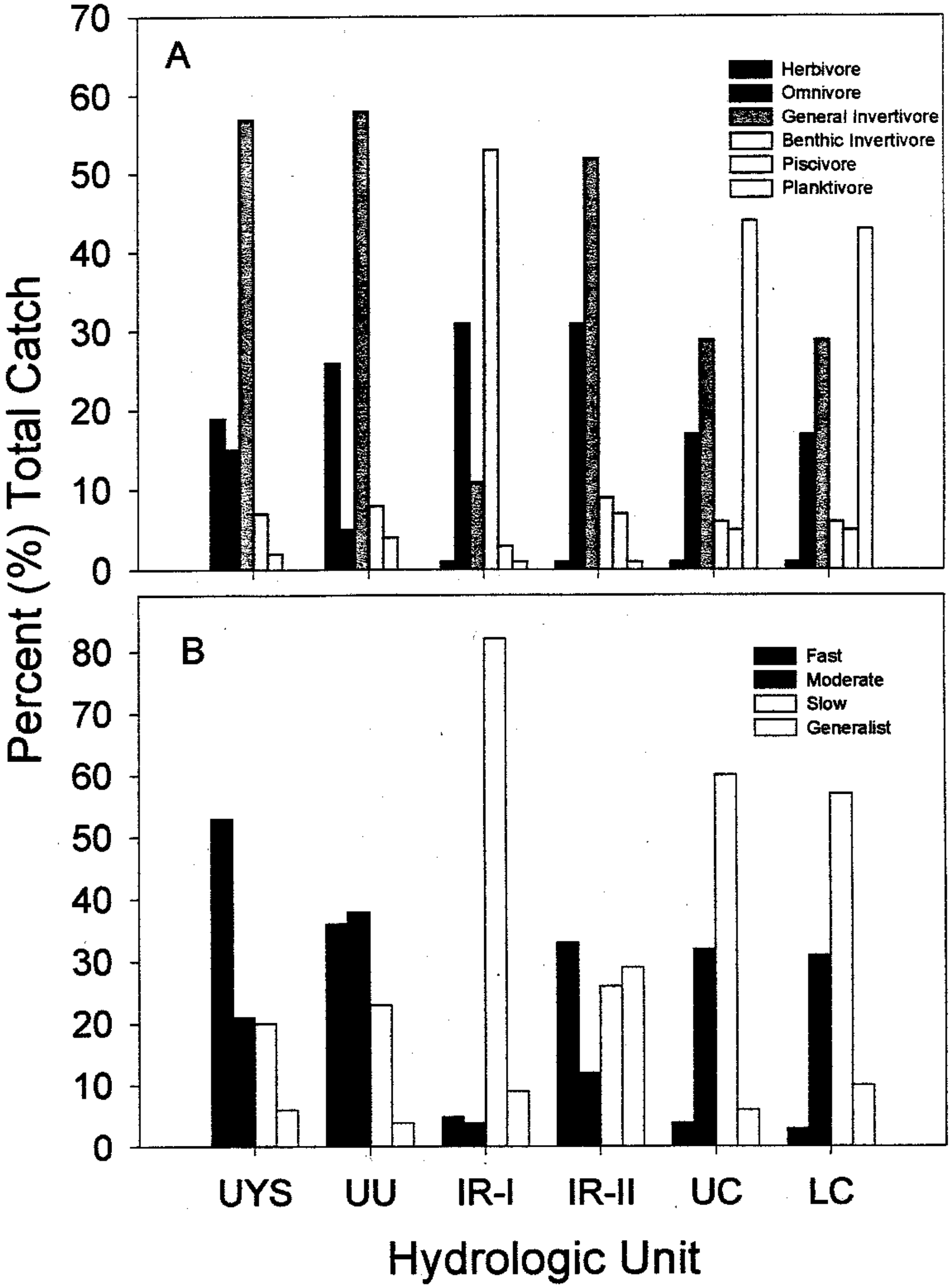

80
60
40
20
0
100
80
60
40
20
0
Number of Species
Large River Species (%)
13,876
9,726
4,807
3,529
13,164
16,694
UYS
UU
IR-I
IR-II
UC
LC
Hydrologic Unit

Figure 3.



A
Herbivore
Omnivore
General Invertivore
Benthic Invertivore
Piscivore
Planktivore
B
Fast
Moderate
Slow
Generalist
Percent (%) Total Catch
UYS
UU
IR-I
IR-II
UC
LC
Hydrologic Unit

Figure 4.

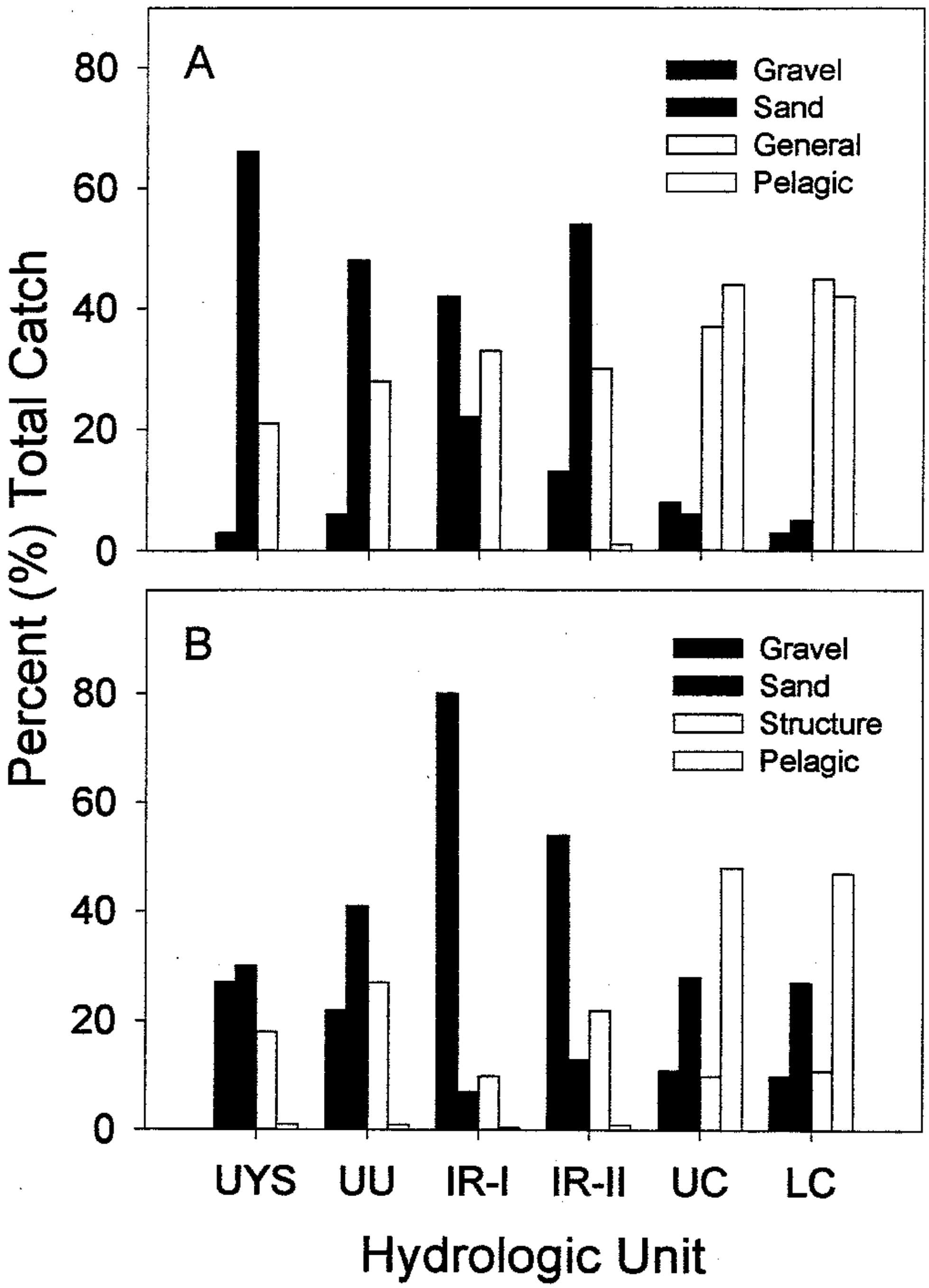

A
Gravel
Sand
General
Pelagic
B
Gravel
Sand
Structure
Pelagic
80
60
40
20
0
Percent (%) Total Catch
UYS
UU
IR-I
IR-II
UC
LC
Hydrologic Unit

Figure 5.

CHAPTER 5. GROWTH RATE RESPONSES OF MISSOURI AND LOWER YELLOWSTONE RIVER FISHES TO A LATITUDINAL GRADIENT

A paper to be submitted to the Transactions of the American Fisheries Society

Mark A. Pegg and Clay L. Pierce

Abstract. Growth is an important element of fish population assessment and management. Several studies have shown that the length and quality (cumulative degree-days) of the growing season is negatively correlated to latitude and that individual fish may need a flexible growth capacity to compensate for a shorter growing season at higher latitudes. We estimated specific growth rates for channel catfish Ictalurus punctatus, emerald shiners Notropis atherinoides, freshwater drums Aplodinotus grunniens, river carpsuckers Carpiodes carpio, and saugers Stizostedion canadense collected in 1996-1998 for nine river sections throughout the Missouri and lower Yellowstone Rivers to assess spatial trends at two life-stages (young-of-the-year and adult). Growth rates for most species were typically significantly different ($P < 0.05$) among sections but showed no river-wide latitudinal trend with the exception of adult emerald shiners that did show a negative relation. However, trends similar to those of emerald shiners do appear likely for the other species on a regional scale. Our results suggest that understanding growth rate responses to latitude along the Missouri River are complex and could have large impacts on the management and conservation of fish communities in this altered system.

Introduction

Fish growth is a fundamental and often critical element of fish population assessment (Jearld 1983; Summerfelt and Hall 1987; Chambers and Miller 1995), and many biotic and abiotic factors can effect growth rates. Among these factors, water temperature is an influential component of growth in fish populations (Picard et al. 1993; Dutta 1994; Oxenford et al. 1994; Radtke and Fey 1996). Because there can be a large thermal gradient from higher to lower latitudes within the geographical range of any species, there is a potential for differences in growth rates among populations. Several studies have made comparisons of physiological responses, including growth rates, to latitudinal variation on fish and other aquatic organisms (Conover and Present 1990; Mina 1992; Conover and Schultz 1995; Gudkov 1996; Schultz et al. 1996; Parsons 1997; Brown et al. 1998). Some of these studies suggest that fish obtain larger sizes in lower latitudes (Carlander 1969, 1977; Modde and Scalet 1985), with the idea that these areas provide more opportunity for growth due to longer growing seasons. Conversely, others have reported lengths comparatively equal to or greater in populations from higher latitudes than their lower latitude counterparts implying faster growth rates to compensate for the shorter growing season (e.g., Isley et al. 1987; Conover and Present 1990).

A flexible capacity for growth may allow a species to counteract negative environmental influences like lower water temperature and a shorter growing season. This compensation acts in the reverse direction of (or counter to) phenotypic expression and has been aptly termed "countergradient variation" (CnGV) by Levins (1969). Countergradient variation has been reported for estuarine zooplankton and invertebrates (Dehnel 1955;

Levinton 1983: Levinton and Monahan 1983; Lonsdale and Levinton 1985), amphibians (Berven et al. 1979), marine fish (Leggett and Carscadden 1978; Conover and Present 1990; Present and Conover 1992), and to a limited extent freshwater fish (Isley et al. 1987; Power and McKinley 1997). Here, CnGV meant these organisms put energy towards body growth over the same temperature range regardless of geographic location, but growth rates were higher to compensate for the shorter growing season at higher latitudes. Some studies even reported that higher latitude fish attain larger sizes than their lower latitude equivalents in the first year of life (Conover and Present 1990; Mina 1992). This may be a function of over-winter, size-selective mortality, because smaller sized individuals may not survive the winter months due to the lack of food storage reserves present in larger individuals (Mina 1992). Oliver et al. (1979) reported that larger smallmouth bass Micropterus dolomieu had higher first winter survival rates over the northern part of their distributional range. Likewise, Conover and Present (1990) reported similar results for Atlantic silversides Menidia menidia where higher latitude individuals grew at least two times faster to attain the same or larger lengths.

Most research focusing on latitudinal patterns in fish growth comes from marine and estuarine systems (Leggett and Carscadden 1978; Conover 1990; Present and Conover 1990; Conover and Present 1992); whereas, freshwater fish have generally not been studied specifically for evidence of latitudinal patterns across their geographic range. Our data from a study on the Missouri and lower Yellowstone Rivers do provide an opportunity to examine longitudinal patterns of growth for several freshwater fish species that come from different phylogenetic groups and varying life histories. Studying species from varying backgrounds provides insight into the broad evolutionary trends that exist in an ecosystem (Conover 1990). Our objectives were to 1) determine area specific growth rates for five fish species from the Missouri and lower Yellowstone Rivers (channel catfish Ictalurus punctatus, emerald shiners Notropis atherinoides, freshwater drums Aplodinotus grunniens, river carpsuckers Carpiodes carpio, and saugers Stizostedion canadense), 2) test for differences among these growth rates, and 3) determine if there is evidence supporting the CnGV phenomenon for these five species.

Methods

Fish and Body Structure Collection

The goal of our sampling design was to quantitatively characterize fish growth throughout the river system. Our sampling protocol divided the river into several spatial scales using a hierarchical framework (Frissell et al. 1986; Hawkins et al. 1993). We collected fish from 17 segments located throughout the riverine portions of the Missouri and lower Yellowstone Rivers during the late summer and early fall in 1996-1998. However, because segment growth data were limited for several of the five species, we focused our growth rate analyses on making comparisons among nine sections, the next higher level within the framework (Figure 1). Sampling gears used included boat electrofisher, beam trawl, bag seine, stationary gill net, and drifted trammel net. Complete details and rationale for sampling design, sampling procedures, data processing, and quality assurance are reported in Sappington et al. (1998).

We collected a variety of calcified structures to determine growth rates from these five species following established methods (Busacker et al. 1990; Devries and Frie 1996). Scales were collected for emerald shiners and river carpsuckers, otoliths were collected for freshwater drums and saugers, and pectoral spines were collected for channel catfish. We followed standardized procedures to prepare each body structure (Jearld 1983; Pegg et al. 1998) and made inter-annual measurements using an image analysis system. Our growth rate estimates required some information on back-calculated lengths at prior ages so we used the Fraser-Lee method to back-calculate lengths at age for river carpsuckers and emerald shiners (Busacker et al. 1990). We used mean inter-annual distance measurements on five scales from each individual and calculated the intercept by regressing scale radius on length at capture. For channel catfish, freshwater drums, and saugers, we used the direct proportion method (Devries and Frie 1996).

Growth Rate Estimation and Comparison

Energy is more readily put towards growth in the first year of life compared to later years when growth is confounded by other energy demands like gamete production (Busacker et al. 1990). Therefore, we placed each individual into one of two life-stage groups that reflected more homogeneous growth: 1) young-of-the-year (yoy) and 2) age-1 and older individuals (adult) for each species.

Our sampling efforts provided an opportunity to catch fish during the growing season throughout the river so we felt it appropriate to estimate growth rates from increases that occurred during our sampling period rather than from estimates based on back-calculation.

Calculating growth rates over the standardized sampling period was also advantageous because we had clearly defined begin and endpoints. This aspect of our rate assessment was beneficial because identifying the precise date of hatch or annulus formation as a growth boundary criterion has been difficult to accurately assess (Machias et al. 1998).

We first estimated species specific growth rates for each life-stage and section. Growth for each individual was calculated as the difference between total length at capture and the back-calculated estimate of length at the start of the growing season (sensu Liao et al. 1995). Conceptually, the growth rate for each section was then estimated by regressing the growth increment data on date of capture during our standardized sampling period (Figure 2). The slope of the regression in Figure 2 is 1.17 mm/d which could then be used for comparisons among the other sections. Our analyses followed this idea, but the actual growth rates were calculated in a slightly different manner. We used analysis of covariance (ANCOVA) to simultaneously estimate slopes of growth on date for all sections (covariate) using the GLM procedure in SAS (Littel et al. 1991). We also used length at the start of the growing season as a second covariate for the adult life-stages to account for size related differences in growth. These slopes, while still reflecting the relative growth rate in each section, are referred to as growth rate coefficients. Next, we tested for differences among growth coefficients using a test for heterogeneity of slopes (Littel et al. 1991).

We then attempted to identify statistically significant trends in growth coefficients with several independent variables that reflected a longitudinal gradient on the Missouri and lower Yellowstone Rivers. These variables included mean sampling latitude, cumulative degree-day, and length of growing season. Mean sampling latitude for each section was determined by calculating the mean latitude from all sampling locations within a section. We obtained unpublished water temperature data from several water treatment facilities, state agencies, and the U.S. Army Corps of Engineers to calculate cumulative degree-days and length of growing season for each section. We then followed methods by Allan (1995) to calculate cumulative degree-days above a threshold temperature of 10°C which encompassed the majority of the growing season for the five species studied. Similarly, we calculated length of growing season as the number of days in which water temperatures were above 10°C.

Results

Length of growing season declined by 27% and cumulative degree-day decreased by 39% from the uppermost to the lowermost sections. Likewise, both degree-day and length of growing season for each section had a strong negative correlation to latitude (Figure 3) indicating that the overall thermal potential decreases with an increase in latitude. Our findings made from analyses using any of the three variables were similar when making large-scale comparisons due to this high correlation. Therefore, we predominantly present latitudinal comparisons to reduce confusion.

Growth Coefficient Estimates

We tested for year effects on the growth coefficients and found significant ($P < 0.01$) among year effects within all species and life-stage categories and thus could not combine data from all three years. The resulting growth coefficients are summarized for each species in Table 1. The negative values shown for some species and sections are largely an artifact of using the covariates in our analyses rather than indicating a negative growth response. Therefore, these estimates should be viewed as relative to growth rates identified in the other sections of the river system rather than absolute growth coefficients. Generally, yoy growth coefficients were higher than the adult life-stages for all species. Growth coefficients also tended to be lower in the areas influenced most heavily by reservoir activity (Sections 2,4, 5 and 6; Figure 1; Table 1) across both life-stage and species.

Channel catfish growth coefficients were estimable for nearly every section, life-stage, and year (Table 1). Comparison of growth rates within sections for each year and life-stage were statistically different ($P < 0.05$) except for yoy estimates in 1996. The coefficients were quite variable among life-stages with the yoy coefficients having typically the highest rates in each section for any given year. The adult estimates tended to fluctuate showing no visually identifiable trend establishing higher or lower coefficients in one area of the river over another.

Growth coefficients were made for emerald shiners at most life-stages and they were significantly different ($P < 0.05$) among sections for most years (Table 1). Estimable coefficients in the upper sections of the river were somewhat limited especially for yoy over the three years of study. However, yoy growth coefficient estimates were generally higher than the adult life-stage.

Growth rate estimates for freshwater drums were sporadic in the upper river among the three sample years (Table 1). The lack of data from the upper river generally precluded making any river-wide comparisons for the yoy and adult life-stages. However, there were no discernable patterns among the yoy life-stage for a given year. Growth coefficients were quite variable for adults among the nine sections with only the 1997 estimates exhibiting significant differences ($P < 0.05$).

River carpsucker growth coefficients were statistically different ($P < 0.05$) and quite variable among the nine study sections for most years and life-stages. When estimates were possible, Sections 5 and 6 tended to consistently have the lowest growth rate. Adult carpsuckers from the lower Yellowstone River (Section 3) were among the fastest growing throughout the river.

Sauger growth coefficients could not be estimated for many sections over the yoy life-stage (Table 1), and tests for differences among sections at either life-stage were largely insignificant ($P > 0.05$). The lack of estimates in many sections was predominantly due to low sample sizes, especially for the yoy fish and the 1996 sampling year. Adult sauger growth rates in the inter-reservoir sections tended to contradict the trend of lower growth observed in the other species analyzed.

Latitudinal Comparisons

We were able to compare growth rates among sections over an 11 degree gradient (Figure 1). Our river-wide tests for latitudinal trends were somewhat inconclusive for four of the five species. While visual inspection of the data may suggest a slight increase in growth rates with an increase in latitude (Table 1), we generally found no statistically significant ($P > 0.10$) latitudinal patterns in the growth coefficients of any life-stage for most species studied. However, growth coefficients for adult emerald shiners did show a relation to latitude and length of growing season (Table 1; Figure 4). Here, the trend was toward higher growth coefficients with an increase in latitude or shorter growing season.

Discussion

We found significant river-wide latitudinal trends only in adult emerald shiners which exhibited increased growth coefficients with higher latitudes along the Missouri and lower Yellowstone Rivers. This suggests that there is some evidence for a CnGV response in emerald shiners. However, we did not find any significant river-wide correlations in the other species studied. There are several explanations that could hinder identification of latitudinal trends. First, emerald shiners were the only species where we could consistently make growth rate estimates in most sections; whereas, consistent estimates for other species were restricted to localized regions. This is largely due to lower sample sizes in some of the upper and middle study sections and is especially prevalent in the yoy analyses for freshwater drums and saugers (Table 1). Therefore, the paucity of data from some sections could hinder our ability to detect a latitudinal gradient in growth coefficients.

Emerald shiners were also the only relatively short-lived species we studied. This may indicate that differences in growth rates along a latitudinal gradient are more pronounced in short-lived species. Growth and growth rates are dependent upon several factors including an individual's growth history. By this, we mean that future growth potential is dependent upon prior growth (Busacker et al. 1990). We collected few emerald shiners beyond age-1 over the course of this study, so it is reasonable that a majority of the growth potential an individual emerald shiner possesses is expressed in the first one to two years of life.

Conversely, the longer-lived species may have a decreased growth potential as they increase in both size and age (Busacker et al. 1990) thereby hiding growth rate differences in variation among individuals of different sizes and ages. A potential bias in growth estimation could result by not taking these ontogenetic shifts into consideration. We did attempt to account for this by using length at the start of the growing season as a covariate in our analyses, but it is possible that this correction did not remove all size biases.

Water management practices such as impoundment and channelization may have influenced growth rates of these fish species along the Missouri River system as well. We did not sample in the reservoirs (Sappington et al. 1998), but some fish were collected in tailwater areas immediately downstream of dams. Sections 2, 4, 5, and 6 are all affected by impoundments in some manner (Chapter 2; Figure 1). Most of these dams are coldwater release facilities that force a localized reduction in the length and quality of the growing season in parts of these sections. Overall, a consistent latitudinal gradient does exist in both length of growing season and cumulative degree days (Figure 3). However, individuals that have been subjected to these localized coldwater releases may have lower growth rates than expected compared to other individuals within the same section. These differences could introduce a sizeable amount of variation within a section thereby clouding any latitudinal trends at the spatial scale we used. Our study does support this theory with many of the lowest growth coefficient estimates coming from the impoundment influenced sections (Table 1).

Channelization may have also forced a shift in growth and other life history characteristics in a non-latitudinal manner. Hesse and Mestl (1993), Pegg et al. (Chapter 2) and Galat and Lipkin (2000) reported that flows along most of the channelized portion of the Missouri River have been drastically altered from their pre-European settlement condition. Some of these changes include higher flow rates, reduced flow variability, and loss of slack water habitats for refugia suggesting a more extreme environment than was historically present. Living under these higher flow conditions likely requires more energy to maintain position in the river and to find food resources. This increased physiological demand can have an effect on many life history characteristics such as a reduced age at maturity (Cardinale and Modin 1999), a younger age structure, and increased growth to attain maturity at an earlier age (Wedemeyer et al. 1990). We do not have site specific information on age at maturity for the Missouri River populations we studied, but the age structure was much younger and back-calculated lengths at age did tend to be higher in the channelized portion of the river for channel catfish, river carpsuckers, and saugers (Pegg et al. 1997) possibly in response to these extreme conditions. Moreover, our higher growth coefficients for these species in the channelized portion of the river add support to the idea of faster growth rates in response to environmental conditions which could have disrupted the natural latitudinal gradient that may have once existed.

Our results could also be confounded by the longitudinal gradient of the biological communities along the Missouri River. Riverine species are highly mobile (Christenson and Blatzenbeler 1996; Pegg et al. 1997) which can inhibit identification of distinct populations via migrations to other locations. Most studies focusing on latitudinal growth responses used distinct populations or strains generally separated by large geographic distances (e.g., Conover and Present 1990; Power and McKinley 1997; Brown et al. 1998). Our study focused on sites where the geographic separation and latitudinal differences between adjacent sections was relatively small (Table 1). Therefore, some interdependency among the fish populations along the Missouri River system is possible and could inhibit clearly identifying large-scale trends in growth coefficients.

While the above explanations describe reasons for the lack of detectable river-wide latitudinal trends in four of the five species we studied, it is possible that variability among individual growth rates was too high to detect any trends. Latitude, degree-days, and length of growing season are not the only variables that influence growth rates. Abiotic factors such as food availability, water velocities, oxygen levels, and biotic interactions in the form of intra- and inter-specific competition are also influential (Wootton 1990). For example, higher growth rates may be advantageous to high latitude populations, but not lower latitude populations due to physiological trade-offs. High growth rates require a large amount of food resources that are not constantly available in the lower latitudes so slower growth rates may prevail in response to fluctuating resources (Conover and Present 1990). Mina (1992) also proposed that smaller fish can better handle the lower oxygen levels that often occur in the lower latitudes as water temperatures rise. Therefore, growth rates are probably the result of a compromise between the adaptation to maximize growth in one environment and the possible poor physiological performance in other environments that may not adhere to a strict latitudinal trend in large, regulated river systems.

Generally, we found few clearly defined river-wide latitudinal trends, but there does appear to be some regional patterns that support CnGV theory. This is most prevalent in the channelized portion of the river in sections 7, 8, and 9 (Figure 1) for channel catfish, emerald shiners, freshwater drums, and river carpsuckers (Tables 1). The latitudinal, growing season, and degree-day gradients are not relatively large among these three sections compared to the entire basin, yet growth rate estimates were consistently higher in section 7. Earlier, we alluded to the fact that management practices may cloud the overall results when trying to detect system-wide trends. This may be true at a river-wide spatial scale but assessment at a regional level may provide insight into growth rates for areas with similar environmental conditions in intensely managed systems. Evaluating growth rates from populations that have been subjected to the same relative conditions over a latitudinal gradient may provide the best *in situ* perspective to detect evidence of counter gradient responses in large systems. The lower, channelized portion of the Missouri River provides such an opportunity and our results do suggest that growth rates are higher in the higher latitudinal reaches.

Conover (1990) identified several implications of CnGV on biological organisms including the fact that many of these organisms have more genetic variation in their capacity for growth than was originally thought. Determining life history traits such as the capacity for growth, as discussed here, is important beyond the evolutionary aspects of how organisms respond to their biotic and abiotic surroundings. Countergradient variation in life history characteristics can also have a serious impact on several disciplines within the fisheries community. For example, selecting brood stocks from a particular population with a higher capacity for growth could be advantageous in controlled aquacultural settings.

Methods used to manage commercial, sport, forage, and threatened or endangered species can also be affected by CnGV. The effectiveness of transplanted or stocked fish, originally from other latitudes, will depend to some extent on their capacity for growth. This is probably most important for restoration efforts on endangered or threatened species as stocking "mal-adapted" individuals can result in poor growth and survival. For example, if individuals originally from the lower latitude of a species' range are stocked in a location near the higher latitude extremes of its distribution, the capacity for growth may not be sufficient to overcome the shorter growing season. Several studies have reported size-selective, over-winter mortality of yoy individuals as a catalyst for size differences among fish populations (Thompson et al. 1991; Hurst 1995; Kirjasniemi and Valtonen 1997). The basic theory is that as the length and severity of winter increase, it is crucial for fish to reach a larger body size to build and maintain fat reserves. Therefore, attempts at stocking fish without the capacity to fully utilize a shorter growing season may result in a population that cannot become well established or survive because they cannot physically cope with the extreme winters in higher latitudes. As more species become threatened in the Missouri River system, as well as in other lentic and lotic systems, the effects of life history differences throughout a species' range will require consideration to properly conduct conservation and restoration efforts.

Assessing growth rates and other physiological responses to latitudinal gradients is emerging as an important aspect in our understanding of fisheries ecology (Conover 1990). Many factors can influence fish growth rates, confounding detection of the CnGV phenomenon. Despite these problems, we did find some evidence of a correlation between growth rate and latitude, albeit at a more regional scale in four of the five species studied. The evolutionary background of these species are quite diverse suggesting that this response goes beyond a single phylogenetic line. Likewise, the impact of CnGV is quite complex and could have far reaching effects on how we perceive and manage fish and other aquatic organisms. As we gain more insight into how organisms respond to latitude and length of growing season, we will also advance our knowledge into the evolutionary and ecological significance of this phenomenon. Accordingly, controlled experiments are needed to further elucidate differences in growth rates on the Missouri and lower Yellowstone Rivers.

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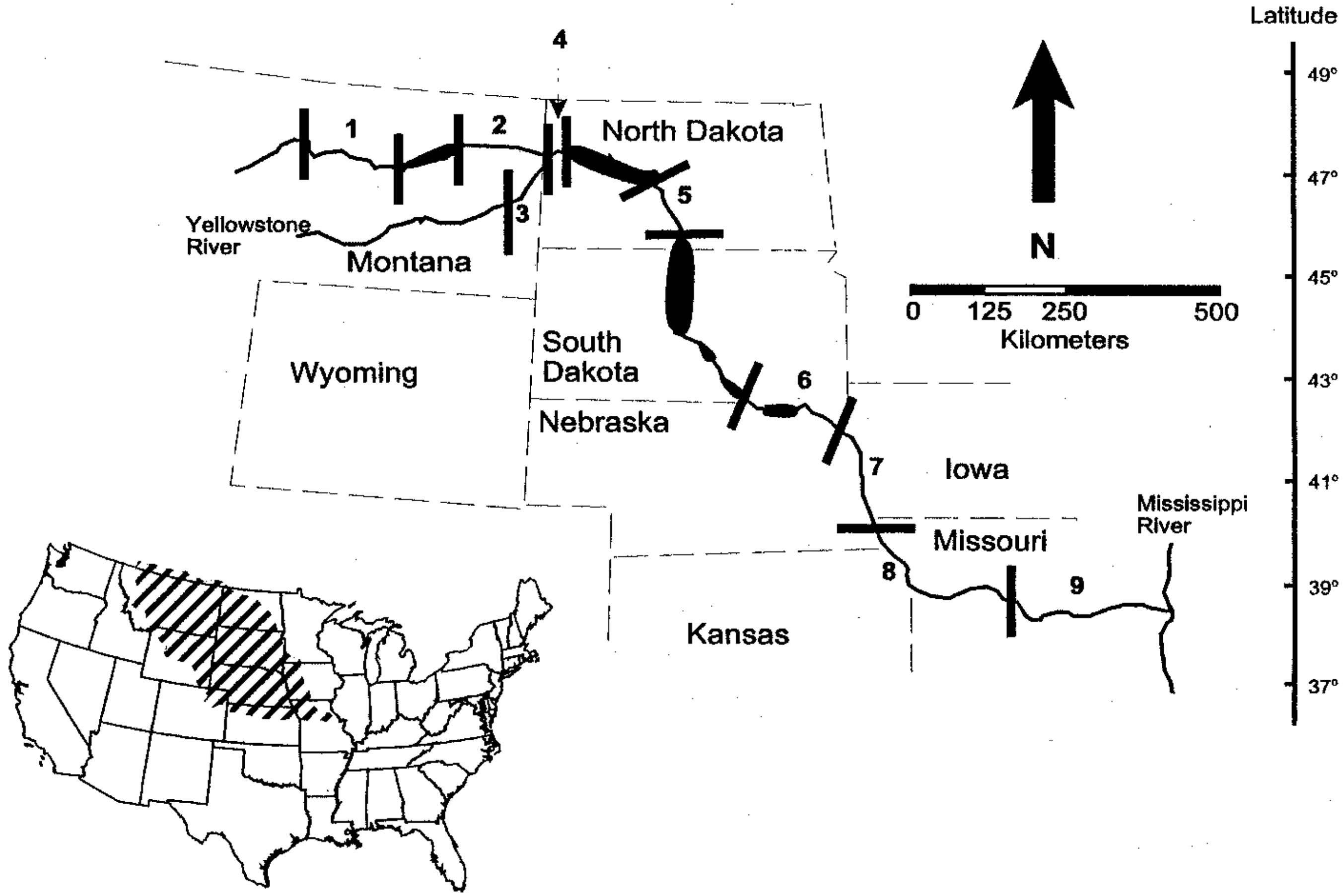
Table 1. Mean latitude, cumulative degree-day, length of growing season, and growth coefficient estimates for five fish species collected throughout the Missouri River basin. Each estimate represents relative growth rates within each sample section. Species specific coefficients are given for young-of-the-year (yoy) and age-1 and older (adult) life stages. Length variability was accounted for in the adult estimates using length at start of the growing season as a covariate. An asterisk (*) indicates the growth coefficients for each section were different ($P < 0.05$) within a given year. Estimates highlighted in bold are significantly different from zero ($P < 0.05$). Sections are arranged from upstream (left) to downstream (right).

Section		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**N**
Mean Latitude		47.4	48.0	47.4	47.6	46.9	42.5	41.2	39.2	38.5	
Cumulative Degree-Day		2783	2800	3141	3005	—	3892	4197	4729	4579	
Growing Season (d)		169	166	173	172	—	197	207	222	233	
Growth Coefficient Estimates											
Channel Catfish (yoy)	1996	—	—	0.34	—	—	1.92	0.18	**0.45**	**0.51**	291
	1997*	0.37	-0.40	0.35	—	—	**0.70**	**0.92**	**0.46**	**0.34**	325
	1998*	0.78	—	**0.55**	—	—	**0.48**	**0.95**	**0.81**	**0.58**	327
Channel Catfish (adult)	1996*	0.85	0.56	0.90	**3.55**	—	0.70	**1.27**	0.22	0.29	191
	1997*	0.02	0.02	0.12	0.30	-0.22	**0.48**	**0.83**	-0.20	**0.22**	680
	1998*	0.25	0.10	**0.52**	0.40	-1.29	0.05	0.53	**-0.30**	-0.01	635
Emerald Shiner (yoy)	1996*	-0.46	—	-0.17	—	—	0.22	**0.64**	**0.21**	**0.14**	821
	1997	0.21	—	0.19	—	—	0.31	**0.52**	**0.32**	**0.37**	737
	1998*	—	0.21	—	—	—	**0.14**	0.25	**0.45**	**0.15**	583
Emerald Shiner (adult)	1996*	**0.12**	—	0.22	—	—	**0.11**	**0.11**	**-0.17**	—	194
	1997*	0.21	—	0.18	0.05	—	**0.13**	**0.23**	**0.10**	-0.50	846
	1998*	**0.12**	**0.05**	**0.27**	0.22	—	**0.09**	0.04	**0.13**	-0.09	697

Table 1. (continued)

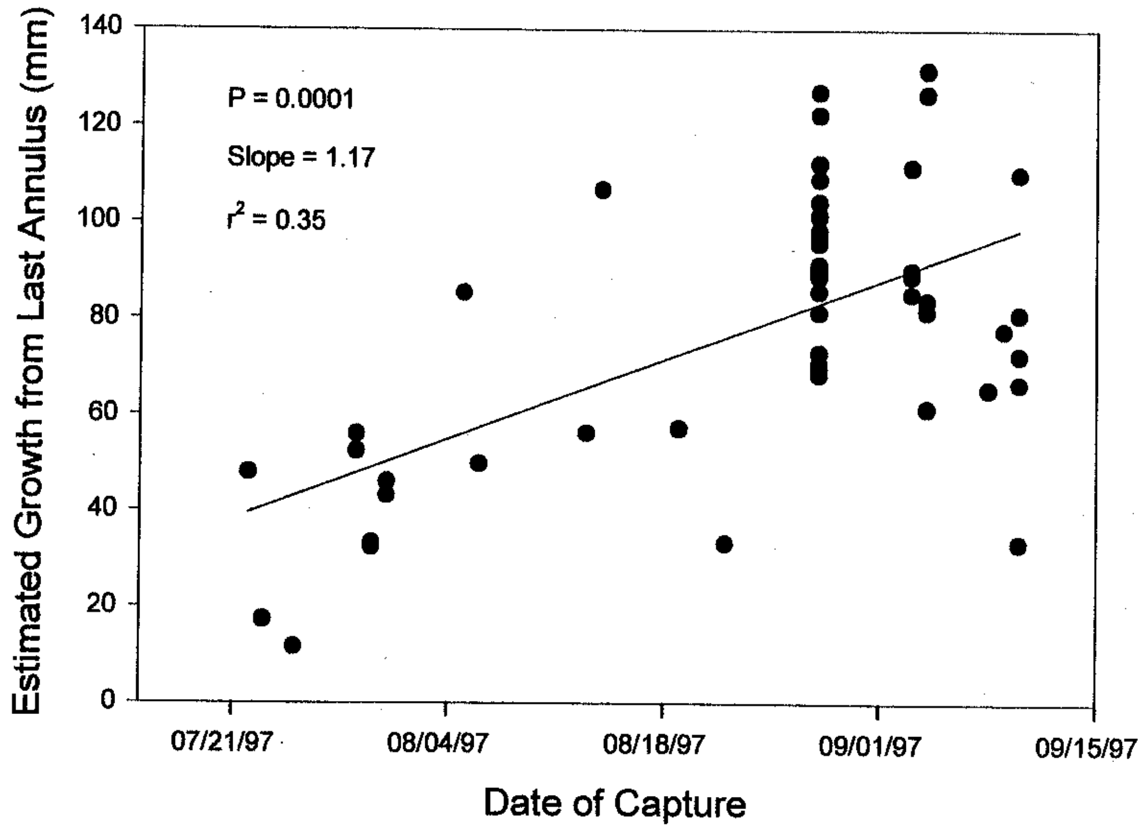
Section		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**N**
Freshwater	1996*	—	—	**2.52**	—	—	**1.81**	**3.66**	**0.37**	**0.77**	274
Drum	1997*	—	—	—	—	—	**1.14**	**3.08**	**0.75**	**0.19**	526
(yoy)	1998*	—	**0.96**	—	—	—	**0.91**	**0.63**	**1.13**	**1.21**	491
Freshwater	1996	0.17	—	—	—	—	**0.44**	**0.38**	**0.30**	**0.43**	205
Drum	1997*	**0.29**	1.37	—	-0.90	—	0.21	**0.99**	0.05	**0.04**	497
(adult)	1998	**0.10**	0.01	**0.32**	0.77	—	**0.11**	0.02	**0.17**	0.07	393
River	1996	—	—	0.23	—	—	**0.50**	**1.09**	0.16	-0.20	148
Carpsucker	1997	0.16	0.14	0.43	-0.17	—	—	**1.21**	**0.51**	**0.59**	313
(yoy)	1998*	**2.70**	0.34	**0.92**	—	—	**0.70**	0.32	0.30	0.05	262
River	1996*	**-0.58**	-0.11	**1.17**	—	-0.31	0.12	**0.38**	**-0.42**	-0.06	200
Carpsucker	1997*	**0.30**	**-0.17**	**0.65**	-0.23	-0.09	0.01	**0.44**	**0.15**	**0.35**	378
(adult)	1998*	0.05	**0.03**	**0.11**	—	**-3.24**	**0.21**	-0.04	**-0.26**	**-0.38**	521
Sauger	1996	—	—	—	—	—	—	**1.67**	—	—	27
(yoy)	1997	**1.17**	—	—	—	—	0.79	—	**1.29**	—	46
	1998	**1.26**	—	—	—	—	**0.85**	—	—	—	68
Sauger	1996*	—	—	-0.78	—	—	—	**0.83**	**0.21**	—	33
(adult)	1997*	0.02	0.15	-0.25	0.25	—	**0.78**	**0.64**	-0.08	—	126
	1998	**0.25**	**0.21**	**0.33**	**-2.60**	1.49	**0.23**	-0.11	**0.43**	0.10	137

List of Figures



Latitude
49°
47°
45°
43°
41°
39°
37°
4
1
2
3
5
6
7
8
9
North Dakota
Yellowstone
River
Montana
Wyoming
South
Dakota
Nebraska
Iowa
Missouri
Kansas
Mississippi
River
N
0
125
250
500
Kilometers

Figure 1.



P = 0.0001
Slope = 1.17
r^2 = 0.35
140
120
100
80
60
40
20
0
Estimated Growth from Last Annulus (mm)
07/21/97
08/04/97
08/18/97
09/01/97
09/15/97
Date of Capture

Figure 2.

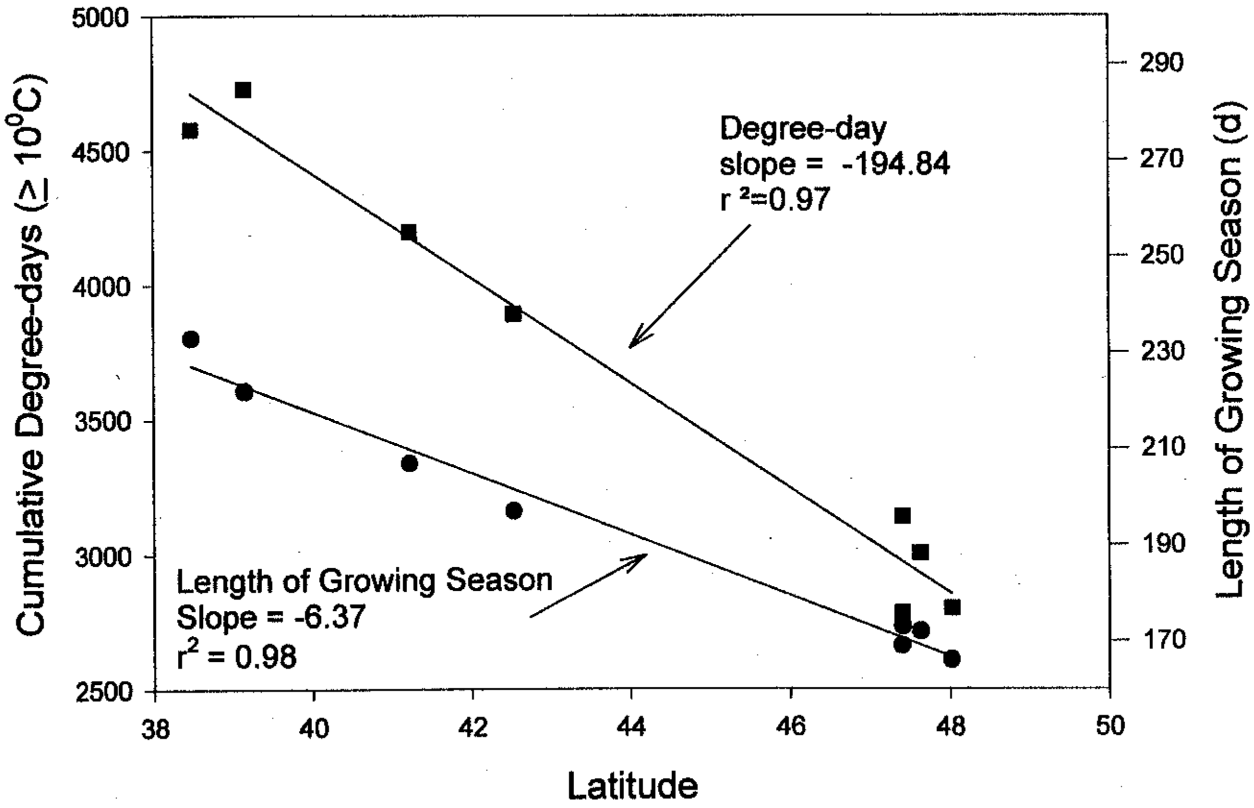

Degree-day
slope = -194.84
r ²=0.97
Length of Growing Season
Slope = -6.37
r^2 = 0.98
Cumulative Degree-days (≥ 10°C)
Length of Growing Season (d)
Latitude
5000
4500
4000
3500
3000
2500
290
270
250
230
210
190
170
38
40
42
44
46
48
50

Figure 3.

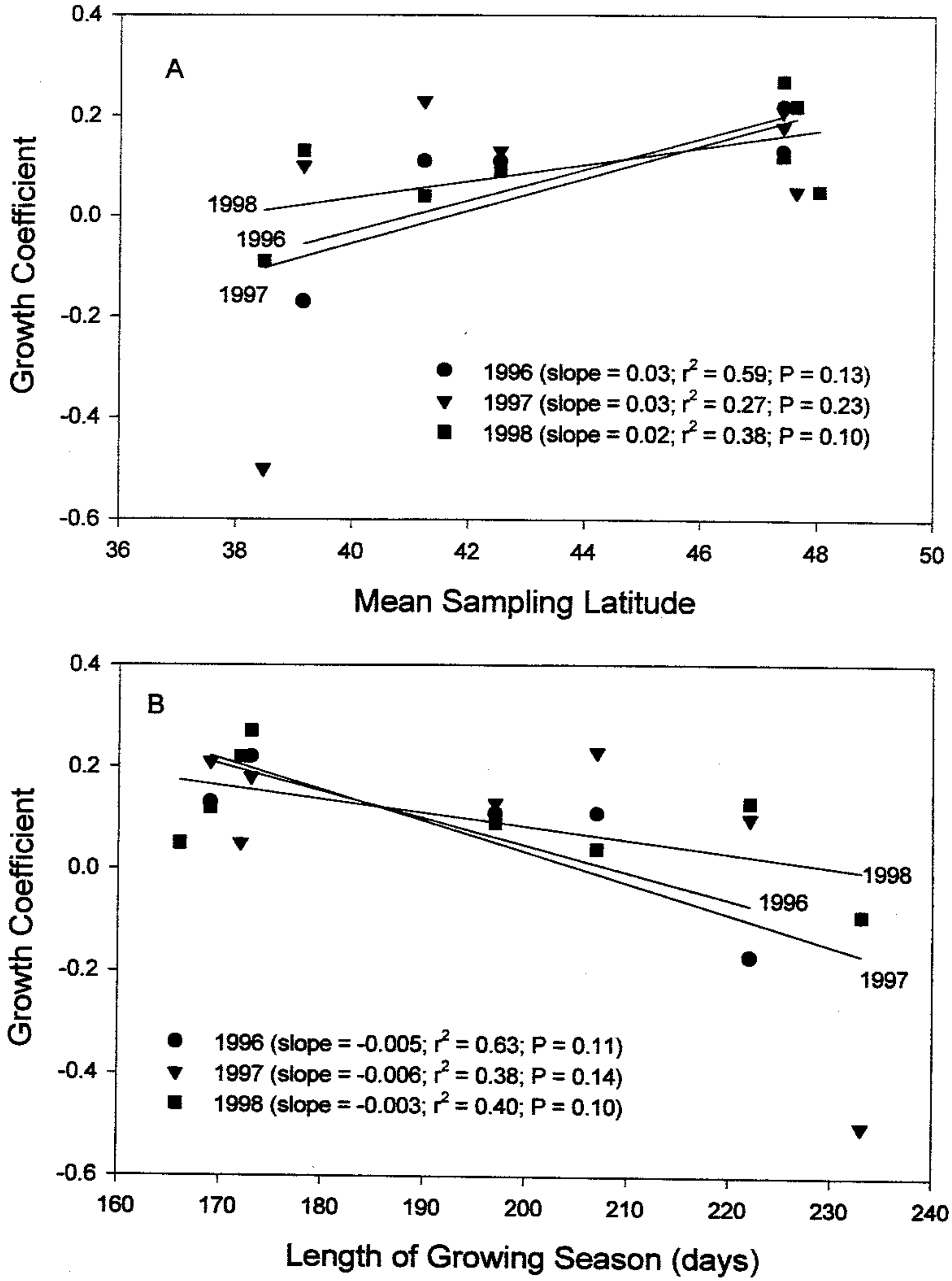

A
Growth Coefficient
Mean Sampling Latitude
1998
1996
1997
1996 (slope = 0.03; r² = 0.59; P = 0.13)
1997 (slope = 0.03; r² = 0.27; P = 0.23)
1998 (slope = 0.02; r² = 0.38; P = 0.10)
B
Growth Coefficient
Length of Growing Season (days)
1996 (slope = -0.005; r² = 0.63; P = 0.11)
1997 (slope = -0.006; r² = 0.38; P = 0.14)
1998 (slope = -0.003; r² = 0.40; P = 0.10)

Figure 4.

CHAPTER 6. GENERAL CONCLUSIONS

General Discussion

Many North American rivers have been altered by humans through construction of reservoirs, channelization, and other flow regulatory mechanisms. Fewer than 50 stretches of free-flowing river longer than 200 km in length remain in the United States (Benke 1990). The Missouri River is one such large system that has been subjected to many alterations and the responses of the biological community to these alterations are not well understood. Reasons for this paucity of knowledge are many but largely center upon the lack of awareness that the ecosystem would be considerably altered during construction of impoundment and channelization structures in the early to mid 20th Century and more recently due to the enormous amount of resources needed to assess the current status of fish in this system. The Missouri River Benthic Fish Project (MRBFP), however, did provide some initial insight into fish populations along the Missouri and lower Yellowstone Rivers.

Through the course of this dissertation, I have built upon the information provided by the MRBFP and addressed three specific topics. First, I investigated aspects of the hydrology along the Missouri and lower Yellowstone Rivers because hydrology is considered an important variable in driving fish community structure. Initially, I evaluated the hydrologic conditions found before and after alteration for 10 gauge stations. Flows were typically higher in the post-alteration period which can probably be attributed to climatological shifts and dam operation through controlled release of flood waters over extended periods. Variability was also lower after impoundment for most of the inter-reservoir and channelized gauge stations. The fact that the hydrograph has changed after major alteration on the Missouri River allowed further investigation into how the fish community has responded to the present flow conditions.

To assess fish communities in relation to flow regimes, I first grouped 15 gauge stations dispersed throughout the Missouri and lower Yellowstone Rivers into six homogenous flow units that reflected the 30 year post-alteration (1966-1996) conditions. Results from this analysis concurred with that of the comparisons between pre- and post-alteration conditions and also with the findings of Galat and Lipkin (2000) that the inter-reservoir and upper channelized units had the lowest amount of variability and was the most altered portion of the river.

There was strong evidence that the fish communities differed among flow units. The ordination results showed a clear separation between the channelized portion of the river from units found above the lowest mainstem dam where species richness estimates were double in the channelized compared to those upstream. These differences were correlated to abundances of several species and to total species richness. Possible explanations for this difference include the prevention of upstream migration through the dams and the altered environmental conditions created by the reservoirs.

Changes to flow conditions can potentially have large impacts on the fish community. Higher flows subject individual fish to more swift velocities that may not be within suitable limits for some species. Likewise, the natural hydrograph has experienced a large reduction in variability after impoundment reducing the occurrence of annual flooding events. These natural spring floods are vital to maintain balanced aquatic communities (Junk et al 1989).

Most native Missouri River species have evolved to capitalize on this natural flooding phenomenon and removal of the spring flood is thought to have caused a general decline in abundances (Hesse 1996). My data provide some evidence supporting this change in species composition in the inter-reservoir units of the river. Many of the large changes in proportion of function groups occurred in the transition into or out of the units highly affected by reservoirs. I also found a higher percentage of generalist species for many of the important life history characteristics (e.g., feeding guild, current preference, spawning substrate preference) in these areas. Moreover, the inter-reservoir units had a much lower component of large river species which dominated the units with a more natural hydrograph. Prospective explanations for this include the encroachment of more lacustrine species from the reservoirs themselves and the establishment of non-riverine species.

Finally, I addressed latitudinal patterns in growth rates of five fish species endemic to the Missouri River (channel catfish Ictalurus punctatus; emerald shiners Notropis atherinoides; freshwater drums Aplodinotus grunniens; river carpsuckers Carpiodes carpio; saugers Stizostedion canadense). Predominantly, I was interested in determining if there was a compensation in growth rate to the shorter growing seasons found in higher latitude areas. While growth rates differed throughout the river for all species, I found an inverse relation between latitude, or length of growing season, and growth rates for only adult emerald shiners. There did appear to be some latitudinal response in the other species, but was evident only in certain regions. This result could be due to the masking factors that widely varying environmental conditions have on evaluating specific, detailed responses at such a large scale.

The topics discussed here are important to river ecology because they provide some insight into our understanding of the complex interactions found in these large river ecosystems that have not been well studied. These subjects are also important because they can provide some prediction on how communities and individuals may respond to various restoration and management techniques. For example, with our knowledge of fish community responses to flow alteration, we may be able to predict changes to community structure as new flow regimes are implemented on the Missouri River. Additionally, latitudinal differences in growth rates could also play an important role as efforts are directed at conserving and restoring native species in the Missouri and lower Yellowstone Rivers.

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